The Eurasian Otter (*Lutra lutra*) in the Alpine Arc: Resource selection and habitat suitability models

---

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Irene Claudia Weinberger

aus

Zug ZG

Promotionskomitee

Prof. Dr. Lukas F. Keller (Vorsitz)

Dr. Fabio Bontadina

Dr. Andreas Kranz

Prof. Dr. Barbara König

Prof. Dr. Margarida Santos-Reis

Zürich, 2016

The Eurasian Otter (*Lutra lutra*) in the Alpine Arc: Resource selection and habitat suitability models

Irene Weinberger

PhD Thesis

Institute of Evolutionary Biology and Environmental Studies
University of Zurich, Switzerland

Content

Summary

Habitat selection is a fundamental aspect in ecology. It affects survival and reproduction of individuals and hence influences population dynamics. Today, most landscapes are modified by anthropogenic activities, resulting in habitat fragmentation, destruction and homogenisation. In such altered landscapes, either species can adapt to the new environmental conditions or they perish. To implement efficient conservation measures, it is crucial to understand how the animals move within a landscape and what habitat requirements they have.

The Eurasian otter (*Lutra lutra*) is a semi-aquatic mammal, whose populations have declined strongly during the 20th century. In recent decades, otter populations started to recover in some areas, e.g. at the periphery of the Alpine Arc. Here the riverine landscape has been altered massively due to hydropower, flood prevention and an increase of road networks and traffic following a strong increase of the human population in the last 30 years. Today, the otter is still absent in large parts of the Alpine Arc. But there are a growing population in the Central Alps in Austria and small and isolated occurrences in the French Alps. Understanding habitat requirements of otters in this landscape and predicting habitat suitability to the core of the Alps will contribute to facilitate the recovery and the reconnection of the populations within the Alpine Arc.

To investigate these aspects, I radiotracked wild otters in the Eastern Central Alps, in Styria (Austria). Using the data of nine otters tracked from seven to 30 months, I analysed habitat selection at multiple spatial scales. Specific behaviours require different habitats. I thus discriminated between the main daily behaviours of foraging and resting. I analysed foraging habitat selection at three different spatial levels: population, individual and within home range (Chapter 2). At the finest scale, I combined habitat selection with movement by applying a step-selection function to the linear system of the watercourses in a novel way. I show that otters adapt well to a landscape interrupted by a multitude of hydropower stations. Indeed, modifications to the riverine landscape by damming provide even new and profitable foraging grounds for the otters. This behaviour may be driven by the traditional fish stocking regime. I conclude that otters are flexible in their selection for foraging habitat, supporting the notion of a successful recovery of the species into the Alpine Arc.

Resting is one of the most vulnerable states of an animal. Resting sites provide protection from harsh weather conditions but also from predators. Humans often evoke strong antipredator behaviour, even in apex carnivores. Little is known about general resting site selection of otters and less about the effect of humans on this selection. As a semi-aquatic mammal, otters are linked to waterbodies and may seek protection in its immediate surrounding. However, modifications to the watercourses and an intensification of the

agriculture have reduced the riparian vegetation. Additionally, leisure activities increase along watercourses. In the third Chapter, I show that resting sites are indeed almost exclusively situated in the riparian vegetation. With data from 284 resting sites, I illustrate that otters are content with small riparian vegetation belts as long as daily human disturbance is low, but that a larger riparian vegetation belt is required as a protective buffer when there are more frequent human activities. I argue that humans are perceived as threats by carnivores and that the intensity of human presence influences resting site selection. I conclude that strips of vegetation cover is a crucial necessity for resting carnivores in anthropogenic altered landscapes and stress the importance of riparian vegetation, a threatened landscape in Europe.

Habitat suitability maps can predict occurrence of a species and provide information on the permeability of the landscape matrix. Scale is an important factor because environmental factors can be scale-sensitive and because conservation actions often are targeted at different levels e.g. local or national. To predict future otter occurrence at the core of the Alpine Arc and its potential to reconnect the French and Austrian population, I developed two habitat suitability models (HSM), using two different data set at a different scale (Chapter 4). The large scale HSM was built on large scale snowtracking surveys in Styria, Austria at a resolution of 10 km^2. For the fine scale HSM I used radiotracking data on resting behaviour, which has higher habitat requirements than foraging behaviour. I demonstrate with both HSMs that there are suitable habitats for otters in the core of the Alps. I show that a recolonization of Switzerland by otters seems possible and a reconnection of the populations within the Alpine Arc is realistic. My results also highlight the importance of scale, which is even more pronounced when environmental data are lacking.

In summary, I evaluated key factors for habitat selection of different behaviours, based on radiotracking data of otters in the Eastern Central Alps. I then used this data to develop habitat suitability models at two spatial scales to reveal the potential of re-expansion of the species to the core of the Alps. In the last chapter (Chapter 5), I summarize my results based on five years of work and discuss my findings, conclusions and their applications.

Zusammenfassung

Habitatwahl ist ein fundamentaler Teil der Ökologie. Sie beeinflusst Überleben und Fortpflanzungsraten von einzelnen Individuen und steuert so die Populationsdynamik der jeweiligen Art. Die meisten Lebensräume sind unterdessen vom Menschen verändert worden, was zu einer Zerstörung, Zerstückelung oder Homogenisierung der Landschaft führt. So müssen sich die meisten Arten an diese veränderten Umweltbedingungen anpassen, oder sie verschwinden. Um Schutzmassnahmen für solche Arten effizient und gezielt einzusetzen, sind Kenntnisse nötig über das räumliche Verhalten in der Landschaft sowie die Anforderungen an den Lebensraum.

Der Europäische Fischotter (*Lutra lutra*) ist eine semi-aquatische Säugetierart, deren Populationen im 20. Jahrhundert massiv eingebrochen waren. Seit wenigen Jahrzehnten jedoch breitet sich die Art wieder aus, so auch in den Alpenbogen. Dort hat sich die Wasserlandschaft stark verändert: Wasserkraftwerke, bauliche Massnahmen zum Hochwasserschutz sowie ein intensives Netz an Strassen sowie einem erhöhten Verkehrsaufkommen beeinträchtigen das Ökosystem Fliessgewässer stark. In den östlichen Zentralalpen (Österreich) wird seit Jahren eine starke Zunahme der Otterpopulation beobachtet und auch im französischen Teil der Alpen mehren sich die Beobachtungen. Bis heute aber ist der grösste Teil des Alpenbogens weitgehend ohne Ottervorkommen. Um die mögliche Wiederausbreitung zu schätzen und die Rückkehr dieser Art zu fördern, sind Kenntnisse über die Ansprüche an Lebensraum sowie die Identifikation von störenden Elementen bedeutend.

Dazu telemetrierte ich wilde Otter in den östlichen Zentralalpen, in der Steiermark (Österreich). Die Daten von neun Otter über einen Zeitraum von bis zu 30 Monaten bilden die Grundlage für die Analysen über die Habitatwahl. Da verschiedene Verhalten auch Unterschiede in der Habitatwahl auslösen, habe ich zwischen der Habitatwahl von Nahrungssuche und Tagesschlafplatz unterschieden. Ich untersuchte die Nahrungssuche auf drei verschiedenen Ebenen: auf der Populationsebene, auf der Ebene des Streifgebietes sowie innerhalb des Streifgebietes. Bei der höchst aufgelösten räumlichen Ebene kombinierte ich die Habitatwahl mit der Fortbewegung des Tieres. Diese so genannte Step-selection Funktion habe ich an die linearen Begebenheiten von Fliessgewässer angepasst. So konnte ich zeigen, dass sich Fischotter gut an die vom Menschen beeinträchtigen Lebensräume anpassen, welche von zahlreichen Kraftwerken durchschnitten werden. Ja, es zeigt sich sogar, dass der Fischotter von diesen baulichen Veränderungen profitieren kann und diese neuen Lebensräume nutzt. Diese Erkenntnisse zeigen ein positives Bild für die Rückkehr des Otters in den Alpenraum.

Schlafen ist eines der verletzlichsten Verhalten eines Tieres. Schlafplätze haben deshalb oft die Schutzfunktion vor schlechten Wetterkonditionen aber auch vor möglichen Räubern. Auch der Mensch wird von vielen Wildtieren als Räuber erkannt und ruft daher starke negative Fluchtreflexe hervor, auch in Raubtieren. Bis jetzt ist relativ wenig über die Schlafplatzwahl von Fischotter in Fliessgewässern bekannt und noch weniger über die Auswirkungen von menschlicher Störung auf die Schlafplatzwahl. Als semi-aquatisches Lebewesen ist der Otter an Gewässer gebunden und somit höchstwahrscheinlich auch an die unmittelbare Umgebung der Gewässer. Allerdings haben bauliche Veränderungen an den Fliessgewässern und die Intensivierung der Landwirtschaft den Uferstreifen stark beeinträchtigt. Aufgrund der Zunahme der menschlichen Bevölkerung wächst auch der Freizeitdruck auf den Gewässerraum. Die Auswertung der Telemetriedaten bestätigte, dass Fischotter fast ausschliesslich in dieser stark bedrängten Ufervegetation übertagen. Meine Resultate zeigen, dass sich Tagesverstecke von Otter in sehr schmalen Ufergürteln finden, sofern es keine menschlichen Aktivitäten rund um den Tagesschlafplatz gibt. Breitere Ufervegetationsgürtel sind aber wichtig, wo menschliche Aktivitäten über den Tag häufig sind. Ich argumentiere, dass Menschen als Gefahr oder Störung erkannt werden und dass die Häufigkeit von menschlicher Störung Auswirkungen auf die Schlafplatzwahl der Otter hat. Meine Schlussfolgerung ist, dass die Vegetation ein wichtiger Schutz für Raubtiere in unserer ausgeräumten Landschaft bietet und dass speziell die Ufervegetation eine wichtige Rolle für viele Raubtiere spielt.

Die Untersuchung von Lebensraumansprüchen bietet die Grundlage für die Modellierung für mögliche Vorkommen. Gute Lebensräumen und deren Durchgängigkeit in der Lebensraummatrix ist zwingend für die Wiederausbreitung einer gefährdeten Art. In den letzten Jahren breitet sich der Fischotter in verschiedenen Regionen Europas wieder aus. Dabei ist eine Vernetzung und Wiederverbindung der Populationen aus Frankreich und Österreich über den Alpenbogen anzustreben. Dazu habe ich zwei Lebensraumeinschätzungen für die Schweiz gemacht, die als Alpenkernland eine Schlüsselrolle spielt. Daten aus der Telemetriestudie bildeten die Grundlage für das hochaufgelöste Modell, während Schneespurenkartierungen über weite Teile der Steiermark die Grundlage für das Modell mit einer Auflösung von $10km^2$ bildete. Beide Modelle zeigten gute Lebensräume in der Schweiz auf, die beide auch eine gute Vernetzung von Ost nach West aufwiesen.

So habe ich also die Lebensraumansprüche von Otter bei zwei verschiedenen Verhalten untersucht und das erworbene Wissen in die Lebensraumanalyse einfliessen lassen. Im letzten Kapitel (Kapitel 5) fasse ich diese Erkenntnisse aus meiner Dissertation zusammen, diskutiere sie und zeige die Anwendbarkeit meiner Resultate auf.

Chapter 1

General introduction

Signs of a species returning to formerly abandoned habitat: Otter tracks in Styria

A changing world

Up to half of the earth' surface has been transformed by humans (Vitousek *et al.* 1997), with mostly negative effects on biodiversity (Fischer & Lindenmayer 2007). Habitat loss, fragmentation and homogenisation are the main threats to native species (Fahrig 2003; McKinney 2006; Brook, Sodhi & Bradshaw 2008; Stoate *et al.* 2009; Krauss *et al.* 2010). Although for most endangered species the futures looks bleak, conservation efforts can be successful, for e.g. species of bats (Hutson, Mickleburth & Racey 2001), koala (McAlpine *et al.* 2006) or gorillas (Robbins *et al.* 2011). With a combination of factors such as legal protection, hazard removal, pollution control, habitat restoration and increasing food availability, some threatened species have recovered or are re-expanding again into historically occupied areas (Lotze *et al.* 2011; Chevallier *et al.* 2015; Hamilton *et al.* 2015). The restoration of mammalian carnivores has been recognized as an successful strategy for biodiversity conservation: They are indicators of landscape-scale conservation success and play an important trophic role (Soule *et al.* 2003). Often, carnivores are used as flagship species for conservation actions for biodiversity (Smith *et al.* 2012).

Due to political and conservation efforts, populations of several carnivore species have started to increase and expand again in recent years, including brown bear (*Ursus arctos*) or Eurasian lynx (*Lynx lynx*) (Breitenmoser 1998; Balestrieri *et al.* 2010). However, the conservation of carnivores is especially challenging because of their relatively large ranges, low numbers and conflict potential with humans (Woodroffe & Ginsberg 1998). Although carnivores are considered to be very sensitive to human disturbances and changes in land-use (Gittleman *et al.* 2001), some carnivore species are able to adapt to a varying degree of fragmentation and urbanisation (Gehrt, Riley & Cypher 2010) with some medium-sized generalists even thriving in highly urbanised areas (Šálek, Drahníková & Tkadlec 2014). There are only few examples of specialist carnivore species which actively move to human modified habitats, either to take advantage from abundant anthropogenic food sources in urbanised areas (Bateman & Fleming 2012) or because the changed landscapes are beneficial to their prey species (Bouyer *et al.* 2014).

In this massively changed and changing world, one of the biggest challenges for conservationist biologists today is to be able to estimate the response of wildlife to anthropogenic change and to predict the consequences of them (Pettifor, Norris & Rowcliffe 2004). It is crucial to understand what are the environmental requirements of a focal species and how individuals move within the landscapes in order to mitigate problems and facilitate the recovery (Whittingham *et al.* 2005). Thus, habitat selection is one of the fundamental aspects in ecology and one of the most urgent matters in conservation due to the continuously shrinking habitat available to many species.

Habitat selection

In this context, often the first questions about an endangered species are: Where does it occur and what are its habitat requirements? Habitat selection is the choice among the resources available made by wildlife, and it differs depending on behaviour. This choice is fundamental for each individual to survive and thrive. Ultimately, it affects population growth rate, abundance and persistence of individuals and species and it shapes community and meta-community structures (Binckley & Resetarits 2005). Habitat selection has been linked to fitness (Manly *et al.* 2002; DeCesare *et al.* 2014) and is framed by niche theory. In this theory, the fitness of individuals is thought as a multidimensional function of biotic and abiotic resources in their surroundings (Hutchinson 1957).
In the ideal free distribution hypothesis (IFD), individuals should strive to live in suitable habitat to increase their fitness. Therefore, it is assumed that individuals - and species - should occupy only suitable habitat – or at least they are to occupy the most suitable habitat prior to unsuitable habitat (Fraser & Sise 1980). The observed deviation of the ideal free distribution is due to the fact that individuals would require perfect knowledge of the available resources and have unlimited dispersal capabilities (Zimmerman, LaHaye & Gutiérrez 2003). However, as all species are limited to some extent, animals of any species are also found in less suitable habitat, even when good quality habitat is still unsaturated (Pulliam 2000). For example, unsaturated suitable habitat is a common trait for recovering populations or invasive species. Nevertheless, population growth and expansion rates ultimately represents the mean fitness among individuals (Mills 2012) and an overall beneficial selection of habitat (DeCesare *et al.* 2014).

Habitat suitability modelling

Research on habitat selection investigates the choice of an animal or a species within a landscape using the perspective of the animal. Habitat suitability models (HSM) or species distribution models (SDM) continue this line of thought of habitat selection but turn the focus around: the resulting map - the habitat suitability map - mirrors the quality of habitat for the species within a given area (Fig.1). These models are important tools in conservation biology to develop management plans and to take decisions to preserve a threatened species or exclude an invasive species. The maps can predict the effects of different climate scenarios and land use changes on the potential occurrence of species (Araújo & Williams 2000; Carone *et al.* 2014), detect areas for reintroduction programs (Halsey, Zielinski & Scheller 2015) and identify conflict zones (Kramer Schadt, Revilla & Wiegand 2005; Bassi *et al.*

2015). Alternatively, the models are used to help detect the occurrence of cryptic or rare species, which are difficult to observe or survey and can provide useful information on the ecological requirements of species (Sattler *et al.* 2007; Mateo-Tomás & Olea 2009). Although the preference to build habitat suitability maps lies on evidence-based research, for species with data deficiencies, such maps are built using the knowledge of experts.

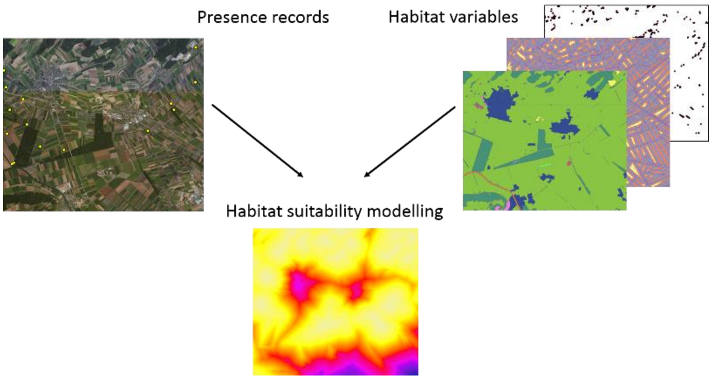


Fig. 1. Process of the habitat suitability modelling

Imperfect data in habitat selection studies

One of the major problems faced in habitat selection and habitat suitability modelling is the imperfect data set, e.g. missing "real absence data". In most ecological studies, the information of the occurrence of a species or individuals is restricted to presence data only. This is also true for radiotracking studies: although the temporal resolution could be set to an extremely high intensity, the GPS devices are usually set on intervals of e.g. 15 min, 2 h or even days, leaving gaps of unknown locations of the animal. These gaps are necessary because a high temporal resolution of data locations of a single individual can induce statistical problems with temporal or spatial autocorrelation and bias the outcome of the study.

Nevertheless, habitat models based on presence-absence data are the most standard approach to habitat modelling (Manly *et al.* 2002). Terms of the designs are usually called "use vs. available" design or "used vs. non-used" and are standard practice in habitat selection studies. In standard logistic regression models the binary response variable is used as indicator if the location was available or non-used (0) or used (1).

As for habitat suitability modeling, presence-only learning machines are often used for presence-only data sets. MaxEnt has become the most commonly used algorithm for habitat suitability modelling. It has been shown to outperform other presence-only techniques (Elith *et al.* 2006), particularly when the amount of presence-data is small (Wisz *et al.* 2008).

Data for habitat suitability modelling usually comes from surveys, monitoring or even specimens in museums. Monitoring occurrence or abundance of species is often done using grids (Donald & Fuller 1998). Generally, these atlases or surveys include equal-sized recording units such as 1 km^2, 10 km^2 or 100 km^2 and are restricted to the spatial resolution at this scale.

The scale in habitat selection

Scale plays an important part in habitat selection studies. Scales can have different meanings in habitat selection. For one, it can address the spatial scale. Spatial scale refers to the resolution of the environmental variables or to the extent of the targeted area. Since some time, it has been acknowledged that environmental variables can be scale-dependent and thus may not provide complete information when only one scale is looked at (Collingham *et al.* 2000; Graf *et al.* 2005). Conservation efforts are often targeted at a specific scale such as national-level or local site habitat management (Cabeza *et al.* 2010) where the extent of the area is defined by politics and not by biological knowledge. Alternatively, the scale can be defined as the biological entity because habitat selection acts on several levels within a population. Johnson (1980) introduced a hierarchical approach for identifying habitat selection at four different scales: 1) the geographical range of the species, 2) the individual home range within the geographical range, 3) patches within the home range and 4) items within the patches e.g. food items (Fig. 2). Thus, the questions on a biological entity will define spatial extent and resolution. Also, the information with the largest resolution defines the overall resolution. Even though the importance and incorporation of the scale in conservation planning is widely recognised, the implementation of multiple spatial scales in conservation management is still rare (du Toit 2010). Indeed, habitat selection studies are often restricted to a coarse spatial resolution because the information is coarse either on species occurrence or on the environmental parameter. The information of the environmental predictors or the species distribution limits therefore the spatial resolution of the analyses. Fine scale models based on detailed species and environmental information have shown to have a great potential to detect crucial habitat structures and are therefore of high interest in conservation. However, such fine scaled information is difficult to obtain and the choice of scale in applied ecology is frequently driven by logistics than concept (Bowyer & Kie 2006). Using a multi-scale approach may compensate this deficit as detecting the most informative scale of analysis is pivotal to understanding habitat selection (Wiens 1989).

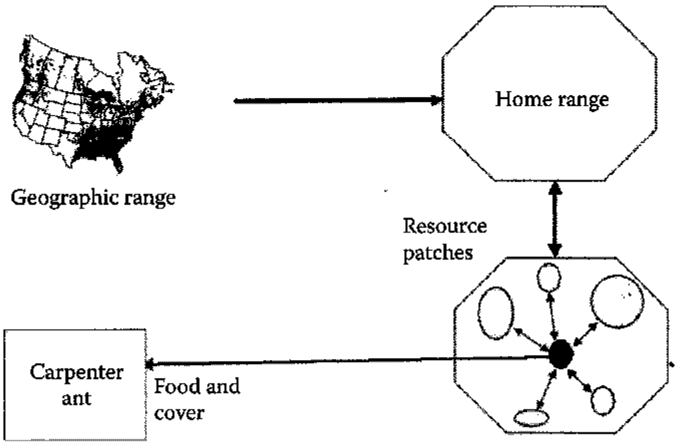


Fig. 2. Hierarchical habitat selection by Johnson (1980), adapted by McComb et al. (2010)

Disappearing landscapes: the freshwater ecosystems in the Alpine Arc

The Alpine Arc is one of the last pristine refuges in Europe, where human impact has been moderate to low up to the 1940s (Perlik 1999). In the last decades, the alpine landscape has been altered massively by humans (Stöcklin *et al.* 2007). Many of the anthropogenic induced changes lead to a decline of bird and wildlife populations, e.g. the mechanisation and intensification of agriculture (Britschgi, Spaar & Arlettaz 2006), urbanization of remote alpine valleys (Scolozzi & Geneletti 2011), increased road network and high traffic volume resulting in fragmentation of habitats (Coffin 2007), barriers (Puky 2005), intensive spare time activities throughout the year (Ingold 2006) and a growing tourism industry (Caprio *et al.* 2011).

Although all ecosystems are affected by climate change and change in biogeochemical cycles (Vitousek *et al.* 1997), the freshwater ecosystems are considered to be among the most endangered worldwide (Dudgeon *et al.* 2006). Virtually all freshwater bodies have been modified to fit the human needs, resulting in physical alterations, habitat loss, water withdrawals, pollution, overharvesting of species and the introduction of non-native aquatic species (see Revenga 2007). Those modifications are especially striking as the freshwater ecosystems harbour an extremely high species richness and endemism (see Revenga 2007).

As part of the freshwater ecosystem, the riparian vegetation is essential for the dynamics and the functioning of the ecosystem. It provides habitat for a disproportionally large amount of species compared to other forested areas (Bennett, Nimmo & Radford 2014). Nevertheless much of the riparian vegetation worldwide has been converted to agricultural lands or destroyed altogether for the benefit of human settlements (see Naiman et al. 1993).

In the European Alpine Arc, much of the watercourses have been altered massively with many running waters being canalized and large parts of the river banks converted from their natural state to artificial or semi-natural borders (Comiti 2012). Although humans have modified the flow of rivers since centuries, the changes have increased in size and amount since the 1900's and still continue today. Additionally since the 1940s, many hydro electrical power stations have been built along the streams and rivers (Comiti 2012), interrupting the free flow of water and sediments and disrupting the movement and dispersal of species. This leads to an alteration and fragmentation of habitat and affects aquatic and semi-aquatic species such as fish and macroinvertebrates but also birds (Bunn & Arthington 2002; Murchie *et al.* 2008). Eventually, those modifications could affect predators depending on aquatic prey such as the Eurasian otter (*Lutra lutra*).

The Eurasian otter in Europe

The Eurasian otter is one among the many species, which experienced a massive decline in the last century in wide areas of Europe. It is listed as "Near Threatened" on the IUCN red list of Europe (Temple & Terry 2007) and is further protected under the EC Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC). Main reasons for the decline are attributed to a combination of habitat fragmentation and loss (Kruuk 1995), environmental contaminants such as PCB, DDE and mercury (Macdonald & Mason 1994) but also to direct persecution. The presence of otters in freshwater ecosystems has been linked to riparian vegetation (Mason & MacDonald 1986; White, McClean & Woodroffe 2003) and high water quality (Roos *et al.* 2001). Therefore the species is often used as an ambassador for pristine and healthy habitat with a low level of tolerance to human disturbance (Bifolchi & Lode 2005).
In the last few decades, populations of this endangered species recover slowly in many areas, where the populations had been reduced or had been even extinct (Kranz & Toman 2000; Janssens *et al.* 2006; Prigioni, Balestrieri & Remonti 2007; Almeida *et al.* 2012). This has led to the development of several habitat suitability models for otters: Europe (Cianfrani *et al.* 2011), Czech Republic (Marcelli *et al.* 2012), France (Van Looy *et al.* 2013), Germany (Klenke 1998), Hungary (Kemenes & Demeter 1995), Italy (Ottino, Prigioni & Taglianti 1995; Prigioni 1995; Remonti *et al.* 2008; Loy *et al.* 2009; Marcelli & Fusillo 2009; Ottaviani *et al.* 2009; Cianfrani *et al.* 2010; Carranza *et al.* 2012; Carone *et al.* 2014) and Switzerland (Cianfrani *et al.* 2013).
Otters in European freshwater ecosystems are nocturnal and elusive, which makes them extremely difficult to study. Their distribution is therefore often assessed using the standard

otter survey methodology, which requires that searches for signs such as faeces (spraints) are conducted along a 600m transect of river bank or lake shore (Mason & MacDonald 1986). This widely used monitoring scheme is designed to assess the distribution of otters at broad scales (e.g. 10km^2), because the probability of detection at a single transect is <30% for a single visit (Parry *et al.* 2013). Almost all HSM for otters are relying on indirect observations such as spraints or expert-based knowledge and are developed at a single scale.

The Eurasian otter in the Alpine Arc

In regions such as the Alpine Arc, the otter was nearly gone extinct with only few individuals remaining at the edge of the Alps (Foster-Turley, Macdonald & Mason 1990). In the last few decades, the otter populations have expanded again (Kranz 2000; Lemarchand, Rosoux & Berny 2011; Kranz *et al.* 2013; Pavanello *et al.* 2015) and the first scouting individuals have been even sighted recently in Switzerland (see www.prolutra.ch), where the species got extinct in 1989 (Weber 1990). To facilitate and estimate the recovery potential, it is crucial to understand the species' habitat requirements and habitat potential in the Alpine Arc.
Little is known about the habitat requirements of the species in this landscape. Information is needed because the freshwater ecosystem has been altered massively since the disappearance of the species in the core area of the Alps. To understand the habitat requirements of this specialist carnivore in this altered habitat, to identify problems of conflict in a landscape dominated by humans and to recognize potential regions for recolonization is fundamental for the survival and return of the species in the long-term.

This study

In this study, the habitat selection of otters in the Alpine Arc and the habitat suitability for otters in Switzerland was analysed at multiple scales. Otters are only slowly coming back to the Alpine Arc, where they will have to live in freshwater systems in a highly anthropogenic altered landscape: only few stretches of rivers and streams are natural, the main part of the freshwaters has modified bank sides and the flow of the rivers is often interrupted by dams for hydropower generation.
Understanding how the animals move and cope within such an altered landscape is crucial to implement conservation measures. Foraging and resting are main daily behaviours and have different habitat requirements. Besides modifications to the watercourses, the degree and

distance to nearest human disturbance may also affect the habitat selections differently. Human disturbances are increasing along the streams and rivers due to the growing human population. This results also in an increase of spare time activities along and within rivers, leading to a denser net of infrastructures accessing freshwater areas. I therefore incorporated different sources of anthropogenic activity in the habitat selection analyses at multiple scales.

Conservation measures for re-expanding species can be efficiently planned and targeted when suitable habitat is identified. A helpful tool is habitat suitability modelling as it can be applied to areas where the species is still absent. However, finding the right spatial scale to detect crucial components is difficult. This uncertainty can be mitigated by applying multiple habitat suitability models. I therefore relied on two different sampling strategies of otter occurrence, resulting in different spatial scales. Fine scale animal data derived from the radiotracking fieldwork in the eastern central Alps in Styria, Austria. There, I and my field assistants radiotracked 9 otters over a period of 6 to 30 months at night and during the day to collect data for the analyses. For the large scale habitat suitability mapping, I relied on snow tracking surveys done in the winters 2010/11 and 2012/13, which were on the standard resolution of a $10km^2$ - grid for the large scale modelling. One of the obstacles arising when applying models across countries is the lack of common environmental data. For riverine landscapes, fine scale data such as river width, naturalness of the river itself and its riparian vegetation is extremely scarce or non-existent in most countries. Finding thus valuable common information on watercourses spanning more than once country proves to be very difficult. Luckily, over 70% of the rivers have been assessed eco-morphologically in Switzerland, using a rather simple protocol (Hütte & Niederhauser 1998). Therefore, for the fine scale habitat suitability model, I assessed the ecomorphology of the main rivers and streams in Styria using the same methodology. This way, I was able to model habitat suitability at two different scales for Switzerland – a vast area where the otter is still largely absent.

While these models give insights of potential suitable habitat for large areas, habitat selection studies can yield results at even finer scales. These can often not be considered at the scale of the habitat suitability models due to the lack of information at a finer resolution. Thus, by addressing habitat selection and habitat suitability maps based on multiple scales and different sampling strategies, this PhD thesis aims to provide insights on otter distribution and recovery potential in the Alps.

Objectives of the thesis

The thesis is structured into the following chapters:

Chapter 2 presents the key foraging habitat selection of wild otters in altered landscapes, with special focus on the alterations of the watercourses and human disturbance on foraging behavior. Over the course of six to 30 months, nine otters were radio-tracked intensively in Styria during the night. I then analysed the habitat selection of otters during their active bouts on three different scales: population scale, home range scale and selection of foraging patches within the home range. I applied a step-selection function method, where habitat selection is combined with movement, to a linear system as the studied otters move almost exclusively within the running waters.

Chapter 3 addresses the selection of day resting sites of otters. The nine otters in Styria were tracked at least twice a week at random times during the day, again from six to 30 months. I studied resting site selection at different scales. I analysed resting site location throughout the year as daily choice using a matched-control design. I then studied the quality of the resting site locations and the choice of the resting site structure with focus on human disturbance at different scales.

Chapter 4 assesses habitat suitability in Switzerland at two different scales: 10 km^2 and < $25 m^2$. Data for the large scale habitat suitability stems from snowtracking surveys of otters in Styria from the winters 2010/11 and 2012/13, where over 33 cells of $10 km^2$ have been monitored during the winter months. The fine scale data is derived from the radio-tracking study mentioned above. However, only environmental variables were incorporated that were available to both regions, Styria and Switzerland. I restricted the fine scale analysis to the resting site selection as this behavioural aspect has higher habitat requirements than foraging habitat selection.

Chapter 5 brings together the information from the three previous chapters and discusses the results from habitat selection of otters in the Alpine Arc: where does the species forage and where does it sleep and what are most likely the conditions behind this selection. I discuss the habitat suitability models and provide perspectives for future research.

References

92/43/EEC. (1992) Conservation of Natural Habitats and of Wild Fauna and Flora.

Almeida, D., Copp, G.H., Masson, L., Miranda, R., Murai, M. & Sayer, C.D. (2012) Changes in the diet of a recovering Eurasian otter population between the 1970s and 2010. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**, 26–35.

Araújo, M.B. & Williams, P.H. (2000) Selecting areas for species persistence using occurrence data. *Biological Conservation*, **96**, 331–345.

Balestrieri, A., Remonti, L., Ruiz-González, A., Gómez-Moliner, B.J., Vergara, M. & Prigioni, C. (2010) Range expansion of the pine marten (Martes martes) in an agricultural landscape matrix (NW Italy). *Mammalian Biology*, **75**, 412–419.

Bassi, E., Willis, S.G., Passilongo, D., Mattioli, L. & Apollonio, M. (2015) Predicting the Spatial Distribution of Wolf (Canis lupus) Breeding Areas in a Mountainous Region of Central Italy. *Plos One*, **10**, e0124698.

Bateman, P.W. & Fleming, P.A. (2012) Big city life: Carnivores in urban environments. *Journal of Zoology*, **287**, 1–23.

Bennett, A.F., Nimmo, D.G. & Radford, J.Q. (2014) Riparian vegetation has disproportionate benefits for landscape-scale conservation of woodland birds in highly modified environments (ed J Wilson). *Journal of Applied Ecology*, **51**, 514–523.

Bifolchi, A. & Lode, T. (2005) Efficiency of conservation shortcuts: An investigation with otters as umbrella species. *Biological Conservation*, **126**, 523–527.

Binckley, C.A. & Resetarits, W.J. (2005) Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biology Letters*, **1**, 370–374.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R.C., Odden, J. & Linnell, J.D.C. (2014) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Animal Conservation*, **18**, 271–278.

Bowyer, R.T. & Kie, J.G. (2006) Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Diversity and Distributions*, **12**, 244–257.

Breitenmoser, U. (1998) Large predators in the Alps: The fall and rise of man's competitors. *Biological Conservation*, **83**, 279–289.

Britschgi, A., Spaar, R. & Arlettaz, R. (2006) Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat Saxicola rubetra: Lessons for overall Alpine meadowland management. *Biological Conservation*, **130**, 193–205.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J. a. (2008) Synergies among extinction drivers

under global change. *Trends in Ecology and Evolution*, **23**, 453–460.
Bunn, S.E. & Arthington, A.H. (2002) Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environmental Management*, **30**, 492–507.
Cabeza, M., Arponen, A., Jäättelä, L., Kujala, H., van Teeffelen, A. & Hanski, I. (2010) Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54–63.
Caprio, E., Chamberlain, D.E., Isaia, M. & Rolando, A. (2011) Landscape changes caused by high altitude ski-pistes affect bird species richness and distribution in the Alps. *Biological Conservation*, **144**, 2958–2967.
Carone, M.T., Guisan, A., Cianfrani, C., Simoniello, T., Loy, A. & Carranza, M.L. (2014) A multi-temporal approach to model endangered species distribution in Europe. The case of the Eurasian otter in Italy. *Ecological Modelling*, **274**, 21–28.
Carranza, M.L., D'Alessandro, E., Saura, S. & Loy, A. (2012) Connectivity providers for semi-aquatic vertebrates: The case of the endangered otter in Italy. *Landscape Ecology*, **27**, 281–290.
Chevallier, C., Hernández-Matías, A., Real, J., Vincent-Martin, N., Ravayrol, A. & Besnard, A. (2015) Retrofitting of power lines effectively reduces mortality by electrocution in large birds: an example with the endangered Bonelli's eagle. *Journal of Applied Ecology*, **52**, 1465–1473.
Cianfrani, C., Lay, L., Hirzel, A.H., Loy, A. & Le Lay, G. (2010) Do habitat suitability models reliably predict the recovery areas of threatened species? *Journal of Applied Ecology*, **47**, 421–430.
Cianfrani, C., Lay, G. Le, Maiorano, L., Satizábal, H.F., Loy, A. & Guisan, A. (2011) Adapting global conservation strategies to climate change at the European scale: The otter as a flagship species. *Biological Conservation*, **144**, 2068–2080.
Cianfrani, C., Maiorano, L., Loy, A., Kranz, A., Lehmann, A., Maggini, R. & Guisan, A. (2013) There and back again? Combining habitat suitability modelling and connectivity analyses to assess a potential return of the otter to Switzerland. *Animal Conservation*, **16**, 584–594.
Coffin, A.W. (2007) From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography*, **15**, 396–406.
Collingham, Y.C., Wadsworth, R.A., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of non-indigenous riparian weeds: Issues of spatial scale and extent. *Journal of Applied Ecology*, **37**, 13–27.
Comiti, F. (2012) How natural are Alpine mountain rivers? Evidence from the Italian Alps. *Earth Surface Processes and Landforms*, **37**, 693–707.

DeCesare, N.J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L. & Musiani, M. (2014) Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology*, **83**, 343–352.

Donald, P.F. & Fuller, R.J. (1998) Ornithological atlas data: a review of uses and limitations. *Bird Study*, **45**, 129–145.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163–182.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., S. Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.

Foster-Turley, P., Macdonald, S.M. & Mason, C.F. (1990) *Otters: An Action Plan for Their Conservation*. IUCN Otter Specialist Group.

Fraser, D.F. & Sise, T.E. (1980) Observations on stream minnows in a patchy environment: a test of a theory of habitat distribution. *Ecology*, **61**, 790–797.

Gehrt, S.D., Riley, S.P.D. & Cypher, B.L. (2010) *Urban Carnivores: Ecology, Conflict, and Conservation*. Johns Hopkins University Press.

Gittleman, J.L., Funk, S.M., Macdonald, D. & Wayne, R.K. (2001) *Carnivore Conservation* (eds JL Gittleman, SM Funk, D Macdonald, and RK Wayne). Cambridge.

Graf, R.F., Bollmann, K., Suter, W. & Bugmann, H. (2005) The Importance of Spatial Scale in Habitat Models: Capercaillie in the Swiss Alps. *Landscape Ecology*, **20**, 703–717.

Halsey, S.M., Zielinski, W.J. & Scheller, R.M. (2015) Modeling predator habitat to enhance reintroduction planning. *Landscape Ecology*, **30**, 1257–1271.

Hamilton, R.J., Bird, T., Gereniu, C., Pita, J., Ramohia, P.C., Walter, R., Goerlich, C. & Limpus, C. (2015) Solomon Islands Largest Hawksbill Turtle Rookery Shows Signs of Recovery after 150 Years of Excessive Exploitation. *Plos One*, **10**, e0121435.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symp Quantitative Biology* pp. 415–427.

Hutson, A.M., Mickleburth, S.P. & Racey, P.A. (2001) *Microchiropteran Bats: Global Status*

Survey and Conservation Action Plan.

Hütte, M. & Niederhauser, P. (1998) Methoden zur Untersuchung und Beurteilung der Fliessgewässer in der Schweiz Ökomorphologie Stufe F (flächendeckend). *MITTEILUNGEN ZUM GEWÄSSERSCHUTZ,* **27**.

Ingold, P. (2006) Freizeitaktivitäten und Wildtiere - Konflikte, Lösungen. *Mitteilungen der Naturforschenden Gesellschaft in Bern,* **63**, 76–98.

Janssens, X., Defourny, P., Kermabon, J. De & Baret, P. V. (2006) The recovery of the otter in the Cevennes (France): a GIS-based model. *Hystrix Italian Journal of Mammalogy*, **17**, 5–14.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Kemenes, I. & Demeter, A. (1995) A predictive model of the effect of environmental factors on the occurrence of otters (Lutra Lutra L.) in Hungary. *Hystrix*, **7**, 209–218.

Klenke, R. (1998) Habitat suitability and apparent density of the Eurasian otter (Lutra lutra) in Saxony (Germany). *IUCN Otter Specialist Group Bulletin*, **19**, 167–171.

Kramer Schadt, S., Revilla, E. & Wiegand, T. (2005) Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? *Biological Conservation*, **125**, 169–182.

Kranz, A. (2000) Otters (Lutra lutra) increasing in Central Europe: From the threat of extinction to locally perceived overpopulation? *Mammalia*, **64**, 357–368.

Kranz, A., Polednik, L., Pavanello, M. & Kranz, I. (2013) *Fischotterbestand in der Steiermark - Schneespurkartierungen 2010-2013*. Graz, Österreich.

Kranz, A. & Toman, A. (2000) Otters recovering in man-made habitats in central Europe. *Mustelids in a modern world*, (ed H.I. Griffiths), pp. 163–184. Bachhuys Publishers, Leiden, Netherlands.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. & Steffan-Dewenter, I. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, **13**, 597–605.

Kruuk, H. (1995) *Wild Otters: Predation and Populations*. Oxford University Press Inc., Oxford UK.

Lemarchand, C., Rosoux, R. & Berny, P. (2011) Semi Aquatic Top-Predators as Sentinels of Diversity and Dynamics of Pesticides in Aquatic Food Webs: The Case of Eurasian Otter (Lutra lutra) and Osprey (Pandion haliaetus) in Loire River Catchment, France. *Pesticides in the Modern World - Risks and Benefits*, 289–310.

Van Looy, K., Cavillon, C., Tormos, T., Piffady, J., Landry, P. & Souchon, Y. (2013) A scale-sensitive connectivity analysis to identify ecological networks and conservation value in river networks. *Landscape Ecology*, **28**, 1239–1249.

Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C. & Airoldi, L. (2011) Recovery of marine animal populations and ecosystems. *Trends in Ecology and Evolution*, **26**, 595–605.

Loy, A., Carranza, M., Cianfrani, C., D'Alessandro, E., Bonesi, L., Di Marzio, P., Minotti, M. & Reggiani, G. (2009) Otter Lutra lutra population expansion: Assessing habitat suitability and connectivity in southern Italy. *Folia Zoologica*, **58**, 309–326.

Macdonald, S.M. & Mason, C.F. (1994) *Status and Conservation Needs of the Otter (Lutra Lutra) in the Western Palaearctic*. Council of Europe Press.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Seletion by Animals*, 2nd Edition. Kluwer Academic Publishers, Dordrecht, Netherlands.

Marcelli, M. & Fusillo, R. (2009) Assessing range re-expansion and recolonization of human-impacted landscapes by threatened species: a case study of the otter (Lutra lutra) in Italy. *Biodiversity and Conservation*, **18**, 2941–2959.

Marcelli, M., Poledník, L., Poledníková, K. & Fusillo, R. (2012) Land use drivers of species re-expansion: inferring colonization dynamics in Eurasian otters. *Diversity and Distributions*, **18**, 1001–1012.

Mason, C.F. & MacDonald, S.M. (1986) *Otters: Ecology and Conservation*. Cambrige University Press, New York.

Mateo-Tomás, P. & Olea, P.P. (2009) Combining scales in habitat models to improve conservation planning in an endangered vulture. *Acta Oecologica*, **35**, 489–498.

McAlpine, C.A., Rhodes, J.R., Callaghan, J.G., Bowen, M.E., Lunney, D., Mitchell, D.L., Pullar, D. V. & Possingham, H.P. (2006) The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: A case study of koalas in Queensland, Australia. *Biological Conservation*, **132**, 153–165.

McComb, B., Zuckerberg, B., Vesely, D. & Jordan, C. (2010) *Monitoring Animal Populations and Their Habitats: A Practical Guide*. CRC Press, Boca Raton, USA.

McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.

Murchie, K.J., Hair, K.P.E., Pullen, C.E., Redpath, T.D., Stephens, H.R. & Cooke, S.J. (2008) Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. *River Research and Applications*, **24**, 197–217.

Naiman, R., Decamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological applications*, **3**, 209–212.

Ottaviani, D., Panzacchi, M., Jona Lasinio, G., Genovesi, P., Boitani, L., Lasinio, G.J. & Jonalasinio, G. (2009) Modelling semi-aquatic vertebrates' distribution at the drainage basin scale: The case of the otter Lutra lutra in Italy. *Ecological Modelling*, **220**, 111–121.

Ottino, P., Prigioni, C. & Taglianti, V. (1995) Habitat suitability for the otter (Lutra lutra) of some rivers of Abruzzo region (central Italy). *Hysterix*, **7**, 265–268.

Parry, G.S., Bodger, O., McDonald, R.A. & Forman, D.W. (2013) A systematic re-sampling approach to assess the probability of detecting otters Lutra lutra using spraint surveys on small lowland rivers. *Ecological Informatics*, **14**, 64–70.

Pavanello, M., Lapini, L., Kranz, A. & Iordan, F. (2015) Rediscovering the Eurasian Otter (Lutra Lutra L.) in Friuli Venezia Giulia and Notes on its Possible Expansion in Northern Italy. *IUCN Otter Spec. Group Bull.*, **32**, 12 – 20.

Perlik, M. (1999) Urbanisationszonen in den Alpen. Ergebnis wachsender Pendeldistanzen. *Revue de géographie alpine*, **87**, 147–165.

Pettifor, R.A., Norris, K.J. & Rowcliffe, J.M. (2004) Incorporating behaviour in predictive models for conservation. *Behaviour and Conservation* (eds L.M. Gosling, & W.J. Sutherland), pp. 198–220. Cambrige University Press, Cambridge.

Prigioni, C. (1995) Guidelines for the feasibility study of reintroduction of the otter Lutra lutra in Italy: the project of the Ticino Valley (North-Western Italy). *Hystrix*, **7**, 255–264.

Prigioni, C., Balestrieri, A. & Remonti, L. (2007) Decline and recovery in otter Lutra lutra populations in Italy. *Mammal Review*, **37**, 71–79.

Puky, M. (2005) Amphibian road kills: a global perspective. *Proceedings of the 2005 International Conference on Ecology and Transportation* p. 14.

Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

Remonti, L., Prigioni, C., Balestrieri, A., Sgrosso, S. & Priore, G. (2008) Distribution of a recolonising species may not reflect habitat suitability alone: The case of the Eurasian otter (Lutra lutra) in southern Italy. *Wildlife Research*, **35**, 798–805.

Revenga, C. (2007) Conditions and Trends of Freshwater Ecosystems and the Challenges to Meet Human Water Needs. *Water and Ecosystems - Managing Water in Diverse Ecosystems to Ensure Human Well-being* (eds C. King, J. Ramkissoon, M. Clüsener-Godt & Z. Adeel), p. 1982. The United Nations University, Hamilton, Ontario.

Robbins, M.M., Gray, M., Fawcett, K.A., Nutter, F.B., Uwingeli, P., Mburanumwe, I., Kagoda, E., Basabose, A., Stoinski, T.S., Cranfield, M.R., Byamukama, J., Spelman, L.H. & Robbins, A.M. (2011) Extreme conservation leads to recovery of the virunga mountain gorillas. *PLoS ONE*, **6**.

Roos, A., Greyerz, E., Olsson, M. & Sandegren, F. (2001) The otter (Lutra lutra) in Sweden--population trends in relation to DDT and total PCB concentrations during 1968-99. *Environmental Pollution*, **111**, 457–69.

Šálek, M., Drahníková, L. & Tkadlec, E. (2014) Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Review*, **2050**, 1–14.

Sattler, T., Bontadina, F., Hirzel, A.H. & Arlettaz, R. (2007) Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. *Journal of Applied Ecology*, **44**, 1188–1199.

Scolozzi, R. & Geneletti, D. (2011) Spatial rule-based assessment of habitat potential to predict impact of land use changes on biodiversity at municipal scale. *Environmental management*, **47**, 368–83.

Smith, R.J., Veríssimo, D., Isaac, N.J.B. & Jones, K.E. (2012) Identifying Cinderella species: Uncovering mammals with conservation flagship appeal. *Conservation Letters*, **5**, 205–212.

Soule, M.E., Estes, J.A., Berger, J. & Martinez Del Rio, C. (2003) Ecological Effectiveness: Conservation Goals for Interactive Species. *Conservation Biology*, **17**, 1238–1250.

Stoate, C., Baldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe - A review. *Journal of Environmental Management*, **91**, 22–46.

Stöcklin, J., Bosshard, A., Klaus, G., Rudmann-Maurer, K. & Fischer, M. (2007) *Synthesebericht NFP 48 Landnutzung und biologische Vielfalt in den Alpen*.

Temple, H.J. & Terry, A. (2007) *The Status and Distribution of European Mammals*. Office for Official Publications of the European Communities, Luxembourg.

du Toit, J.T. (2010) Considerations of scale in biodiversity conservation. *Animal Conservation*, **13**, 229–236.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.

Weber, D. (1990) *Das Ende des Fischotters in der Schweiz - Schlussbericht der 'Fischottergruppe Schweiz' 1984-1990*. Bundesamt für Umwelt, Wald und Landschaft, Bern.

White, P.C.L., McClean, C.J. & Woodroffe, G.L. (2003) Factors affecting the success of an otter (Lutra lutra) reinforcement programme, as identified by post-translocation monitoring. *Biological Conservation*, **112**, 363–371.

Whittingham, M.J., Swetnam, R.D., Wilson, J.D., Chamberlain, D.E. & Freckleton, R.P. (2005) Habitat selection by yellowhammers Emberiza citrinella on lowland farmland at two spatial scales: implications for conservation management. *Journal of Applied Ecology*, **42**, 270–280.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H. & Guisan, A. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763–773.

Woodroffe, R. & Ginsberg, J.R. (1998) Edge Effects and the Extinction of Populations Inside Protected Areas. *Science*, **280**, 2126–2128.

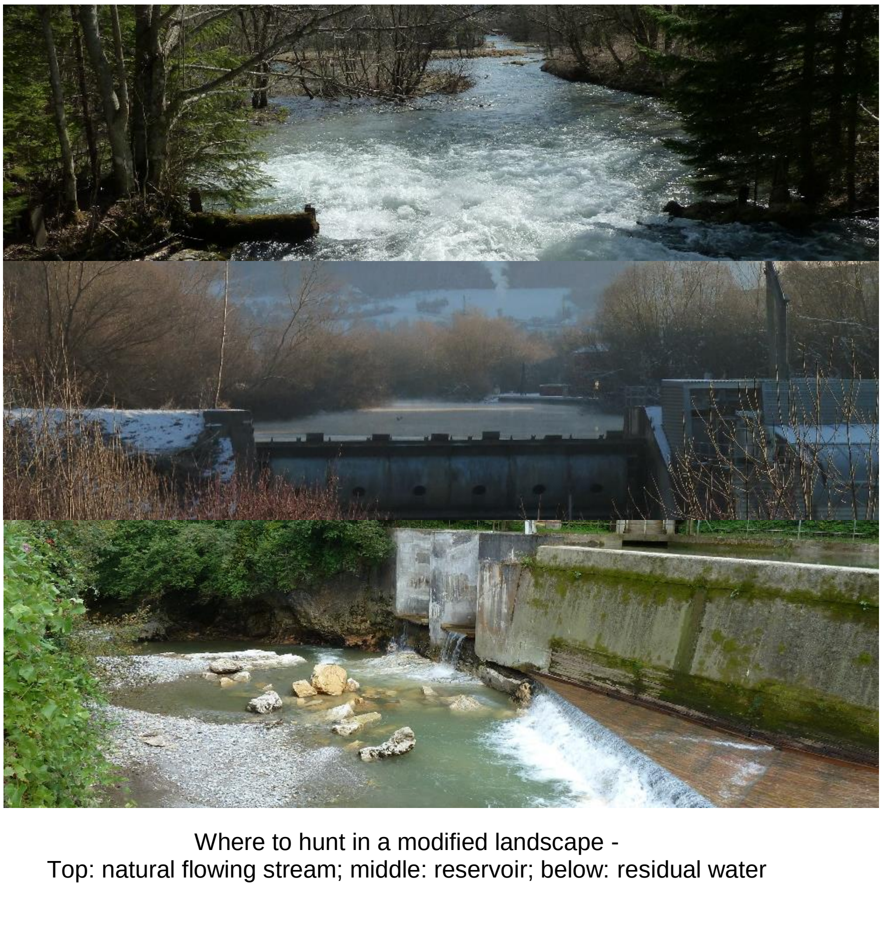
Zimmerman, G.S., LaHaye, W.S. & Gutiérrez, R.J. (2003) Empirical support for a despotic distribution in a California spotted owl population. *Behavioral Ecology*, **14**, 433–437.

Chapter 2

Flexible habitat selection paves the way for a recovery of otter populations in the European Alps

Irene C. Weinberger, Stefanie Muff, Addy de Jongh, Andreas Kranz & Fabio Bontadina

Published in Biological Conservation (2016), 199: 88-95



Where to hunt in a modified landscape -
Top: natural flowing stream; middle: reservoir; below: residual water

Abstract
Carnivores are threatened worldwide through habitat loss and persecution. Habitat destruction is a major threat for the Eurasian otter. Its populations declined drastically in Europe but are now expanding again, including into the Alps. Here, flood prevention and hydropower have massively altered the riverine landscapes.

We evaluated the recovery potential of otters by testing the impact of major factors of habitat transformation and human disturbance on multiple spatial scales. In a hierarchical approach, we investigated spatial use and foraging habitat selection of nine otters in a long-term radiotracking study in the eastern Central Alps. We combined fine scale habitat selection analysis with individual movements by applying a step-selection function approach to the linear river system in a novel way.

At home range scale, otters preferred the main riverbeds to abstracted water and tributaries, whereas at fine scale, there was no significant preference for pristine sections within the watercourses. Otters selected for reservoirs in streams with a width smaller than 12 m and otherwise preferred foraging in residual waters and stretches with main discharge.

At this stage of recovery, otters show a surprising flexibility in their habitat selection. This is promising for the species' future expansion into former abandoned areas. However, given that the traditional fish stocking regime might contribute to this recovery by providing profitable hunting grounds after stocking events, there is an increased risk of human-wildlife conflicts. Our results demonstrate a high adaptability of a threatened carnivore to altered landscapes and show how this flexible behaviour opens opportunities for recovery.

Key words
Lutra lutra, foraging, hydropower plant, radio telemetry, step-selection function

1. Introduction

Environmental change due to human activities is one of the major threats to biodiversity (Vitousek *et al.* 1997). Carnivore species are considered to be especially sensitive to changes in land-use and to human disturbances due to their large spatial requirements, dietary specialisation and low reproduction rate (Ripple *et al.* 2014). With factors such as legal protection and habitat restoration some threatened species have recovered or are re-expanding again into historically occupied areas, e.g. Eurasian lynx (*Lynx lynx*) and wolf (*Canis lupus*) (Chapron *et al.* 2014). However, due to the massive anthropogenic impact worldwide, species have to adjust to habitat transformation and high levels of human disturbance. Changes in habitat structure often alter the availability of resources like food, which in turn requires behavioural plasticity in combination with altered habitat selection or acceptance of novel food resources (Contesse *et al.* 2004). Positive population trends of some carnivores like cougar (*Puma concolor*) or lynx have shown that those species are far more adaptable to using modified landscapes than previously anticipated (Knopff *et al.* 2014; Bouyer *et al.* 2015). It is therefore crucial to understand the adaptability of a species to altered landscapes and its selection of habitats within them to implement conservation measures.

One of the species returning to former areas of its distribution is the Eurasian otter (*Lutra lutra*) (e.g. Elmeros et al., 2006; Ferna, 1998; Kranz and Toman, 2000; Prigioni et al., 2007). The otter is a semi-aquatic carnivore with an almost exclusive specialisation in fish (Krawczyk *et al.* 2016). The otter is therefore closely linked to the existence of aquatic habitat.

In the last century, otter populations have declined in many parts of Europe, resulting in large-scale extinction (Foster-Turley, Macdonald & Mason 1990). A major cause for the decline, beside excessive hunting and the nowadays heavily restricted PCBs, is attributed to habitat deterioration and loss due to river regulations, dam constructions and modifications to the riparian landscape (Kruuk 1995). Today, the otter is classified as “Near Threatened” according to the IUCN red list (Roos *et al.* 2015). In recent years, the species is expanding its distribution again and individuals have even been reported to settle in heavily modified landscapes (e.g. Kranz & Toman 2000; Kloskowski, Rechulicz & Jarzynowa 2013). This has challenged the notion of the otter being a flagship species of pristine and healthy environments (Bifolchi & Lode 2005; Reid *et al.* 2013) and it has raised questions of what kind of habitats they select within anthropogenic altered landscapes. Although the Eurasian otter is the most thoroughly studied otter species (Kruuk 2006), so far only a few studies have addressed the ecology of otters in modified landscapes (Sales-Luís, Pedroso & Santos-

Reis 2007; Weber 2011; Kloskowski, Rechulicz & Jarzynowa 2013; Bueno-Enciso *et al.* 2014; Pedroso, Marques & Santos-Reis 2014).

Since the late 1990s, a growing otter population is re-expanding into the eastern Central Alps (Kranz *et al.* 2013; Kranz & Polednik 2015). Within less than two decades, the species has recolonised the Austrian state of Styria (Kranz & Poledník 2012), with an estimation of 2.8 individuals / 10 km^2 (Kranz *et al.* 2013). This is surprising as the valley bottoms in the Alpine arc belong to the most recent and rapidly transformed landscapes in Europe (Stöcklin *et al.* 2007). Here, a multitude of hydropower plants strictly regulates the flow regime of the rivers. Large parts of the watercourses have been altered by channelisation and most of the natural river banks have been converted to revetments (Comiti 2012). In the last century, much of the riparian vegetation has been reduced, converted to agricultural lands or replaced by human settlements (Naiman, Decamps, & Pollock, 1993). Despite increasing efforts to restore watercourses, riparian vegetation remains very restricted and under ongoing anthropogenic pressure (Comiti 2012). These alterations of the riverine ecosystem have strong negative effects on the aquatic fauna such as the abundance of fish (Bain, Finn & Booke 1988) and as a consequence on otter distribution (Kruuk 1995).

Human presence has been shown to have adverse effects on otters (Prenda, Lopez-Nieves & Bravo 2001; Juhász *et al.* 2013) but has been questioned as a general cause for disturbance (see Kruuk, 2006). Females can exhibit a higher sensitivity to humans as shown in other mammals, because females choose more remote and pristine habitat for reproduction (Ramesh, Kalle & Downs 2015). In the Alps, main roads are often close to the watercourses in the valley ground. Additionally, humans visit riparian landscapes for their spare time activities, thus probably influencing spacing behaviour of otters.

The objective of this work was to assess the habitat preferences of otters at different scales in a region with a mosaic of modified and natural stretches of watercourses, abstracted waters for hydropower use and standing waters such as ponds. We were especially interested in understanding if modifications of watercourses and human disturbance affect foraging habitat selection of otters. In natural watercourses, fish biomass per m^3 decreases with increasing river width (Schager & Peter 2001), and is lower in regulated stretches than where the water flow is natural (Fette *et al.* 2007). Therefore, we expected otters to prefer the most natural stretches at any given scale because fish biomass modulates presence of otters.

We analysed habitat selection at three scales: population, home range and within home range (Johnson 1980). At the population scale, we expected a sex-specific difference in the location of home ranges, with territories of females in less disturbed areas. At the home range scale, we predicted that otters mainly forage in the main riverbed or in standing water such as fishponds where fish densities are high. At the fine scale, we expected otters to forage in the most natural parts of rivers while avoiding regulated stretches.

Most models for habitat selection assume that the animals move freely within the landscape. However, many species are restricted in their movements to quasi-linear features, like hedges or rivers. For those species, the analyses using methods based on two-dimensions may not capture their real habitat selection in relation to the perceived habitat availability and the results may be biased. Fortin *et al.* (2005) introduced the step-selection function method, where habitat selection analysis is combined with the species-specific animal movement pattern. To identify fine-scale foraging habitat selection, we developed a novel approach to apply a SSF to the linear system of watercourses.

2. Methods

2.1 Study area

The field study was conducted from May 2010 to March 2013 in the eastern Central Alps in Styria, Austria in the area of Bruck an der Mur (N47°24'36", E15°16'7"; Fig. 1). The area covers approximately 1760 km^2, with about 3090 km length of watercourses. All rivers and streams in the study area belong to the catchment basin of the river Mur, which has a mean annual discharge of 110m^3/s. The main valley in the study area is named after the river Muerz (mean annual discharge: 20m^3/s). The waters are mainly inhabited by brown trout (*Salmo trutta*) and European grayling (*Thymallus thymallus*). The area at lower attitude is dominated by iron industry, intensive agriculture and urban areas. In the secondary valleys, the landscape changes to agriculture and forests. The elevation of the valley floor ranges from 458 to 974m, with the surrounding mountains up to 1850m. The rivers Mur and Muerz and the larger streams are channelled in large parts and dammed for electrical power generation (dams heights up to 5 – 10m; Fig. 1).

2.2 Radio telemetry

Otters were trapped with soft-catch traps (No. 3, Oneida Victor Inc., Cleveland, Ohio) coupled with GSM trap alarms (Ó Néill *et al.* 2007). Captures took place in spring and autumn between 2010 and 2012 (Table A1 supplementary material). Trapping actions lasted from five to seven nights. During a given trapping action, traps were set in four to six locations. On average, one otter was caught within 32 trap nights. Once caught, the otter was removed from the trap within 30 minutes of capture and put into a solid transport box. Intraperitoneal implantation of the transmitter (model 325/L, 42g, 9.4 x 2.3cm, life span ca. 15 months; model 400/L, 95g, 9.7 x 3.3 cm, lifespan ca. 31 months, Telonics Inc., Mesa,

Arizona) was carried out in a nearby vet-ambulance after the animal had been sexed and its age estimated. For recovery, otters were kept in a box at a quiet place. All otters were released within 24 hours at the location of capture. Animals were then tracked in bouts between sunset and sunrise by a single person on foot and from car using a receiver (Sika, Biotrack Ltd, Dorset UK), a handheld 3-element Yagi-antenna and an omnidirectional antenna placed on the car roof. Tracking bouts ranged from 90 to 945 minutes (mean=340 minutes) and covered at least one whole night per month per individual. Within bouts, the location of the focal animal was taken every 15 minutes. To increase independent locations, animals were additionally tracked 1-2 times every week at random times at night for two consecutive locations. Day resting sites were located at least twice per week. The observer used a GPS (extrex H, Garmin Ltd) for his location and took the bearing to the animal with a handheld compass. For every observation, activity of the animal was deduced from the variation in signal strength 3-5 minutes before taking the bearing and by comparing location and strength of the signal to the previous and the following bearing. Activity was classified into three categories: (1) active, (2) passive and (3) unknown. The accuracy of the location of the animal was estimated by the observers using the distance to the animal, the spread of the signal and short-term cross-triangulations done by the observer. The accuracy was categorised as within (1) 10m, (2) 20m, (3) 50m, (4) 100m and (5) more than 100m of the estimated location.
The location of the animal was then calculated in ArcView 3 (ESRI 2002) using the bearing and the location of the observer. Animals were tracked until the sender failed, the animal disappeared or until field study ended in March 2013 (Table A1). Trial runs to estimate tracking error were conducted at night during the study with the same materials. There, a transmitter was positioned at the bank side at various distances to the observers. Observers estimated the accuracy for each fix with the mentioned categories above. Tracking error and estimated accuracy were visually compared using boxplots. Tracking error data was congruent for the different classes of accuracies. Locations with accuracy >100m and data from the first ten days after surgery were excluded for all analyses.

2.3 Habitat selection at population level

For the habitat selection at the population level the available area was constructed as a 100% minimum convex polygon (MCP) using ArcGIS 10 (ESRI, 2011). Habitat categories were designated as main river (watercourses ≥4m width) and tributaries (watercourses <4m width) (Table 1a). Individuals were considered as the sample units. Habitat selection was assessed with an Habitat Selection-Index (HS-Index) based on the Jacobs-Index (Jacobs 1974) with the formula

$$HS = (u-a)/(u+a-(2u*a))*100$$

where u is the proportion of the resource used and a the proportion of its availability. Values for HS range from 100 to -100 (maximum preference to avoidance). Habitat type was considered to be significantly selected when its mean value on the Jacobs Index was different from 0 and the 95% credible intervals did not encompass 0. Analyses were done using a Bayesian approach with the package `arm` in `R 3.2.2` (R Development Core Team, 2015).

2.4 Home range size and habitat selection at home range level

For home range estimations, active and passive locations were included in the analyses (with resting sites only once). Two home range estimators were used to calculate availability of habitats in `R`: 95% fixed kernel density contours by the package `adehabitat` (Calenge 2006) and 95% local convex hulls by the package `t-locoh` (Lyons, Turner & Getz 2013). The results of the different estimators were compared using a t-test. As otters foraged in or along water bodies, the actual home ranges used here are the waters within the calculated home range. Foraging habitat selection was assessed exclusively with active locations outside resting sites. The dataset for this analysis was further subset by using locations that were sampled at least 24h apart to reduce spatial autocorrelation. A used-availability design was applied, where availability of habitat was estimated by a set of random locations that was 10 times larger than the number of used locations. The random locations where drawn using the standard toolbox in ArcGIS 10, setting the extent of the area to the home range given by the kernel density estimator. Habitat was classified into four categorical habitat types: (1) main riverbed (including main discharge, reservoirs and residual waters), (2) “abstracted water” (the power plant channel and the downstream water outlet), (3) tributaries and (4) standing water (Table 1b, also see Fig. A1). A logistic regression model with habitat type as covariate and animal as random effect was fitted, where the binary response indicated whether the habitat was available (0) or used (1).

2.5 Foraging habitat selection within home range

The main riverbed was divided into three habitat functions (a) main discharge, (b) reservoir and (c) residual water (Fig. A1) and its ecomorphology was assessed (BUWAL 1998). At the fine scale we included the following variables that have shown to be important for otter presence in other studies: water width, water depth, bank type, bank reinforcement type, riparian vegetation type and riparian vegetation width. We additionally included distance to roads (proxy for human disturbance), distance to hydropower plant (source of fragmentation), distance to fishponds (patch of abundant food) and the presence of wood and algae in the water as it is beneficial to fish (Hafs *et al.* 2014). This information was attributed to the shapefiles of water bodies obtained by the Austrian Department for Meteorology. All predictor covariates are listed in Table 1c. Continuous covariates were centred and scaled. The interaction between habitat category of the main riverbed and river width was added to the model as the potential fragmentation of rivers could be more pronounced in small rivers than in larger ones. Moreover, random slopes for all covariate parameters to account for inter-individual differences were included in the model.

Fine-scale habitat selection was then assessed with a conditional use-availability design (Manly *et al.* 2002). To obtain a resource selection function (RSF) we applied a step-selection function approach (Fortin *et al.* 2005; Thurfjell, Ciuti & Boyce 2014), where observed steps (the linear segment between two consecutively observed points) are compared to a set of random steps with the same starting point. To generate the random points, we followed the protocol of Fortin *et al.* (2005), where random steps for a given starting point differ in length and direction, and the average distribution of step lengths and angles for a given animal is determined based on the distributions of all the other individuals. From those two distributions, random steps were drawn independently. This protocol allows the animal to move in every direction. Species that move along linear features are, however, restricted in their potential paths. In our study area, the otters moved mainly along rivers and streams with rare excursions to ponds near the riverbed. Therefore, we set up a linear network with the extension “Network Analyst” in ArcGIS 10 along all watercourses. As the distribution of the angles is inherently given by the linear system (i.e. only forward and backward movement is possible) only the distribution of the step lengths was used. Where watercourses enlarged to more than double their size (e.g. when entering a lake), we built a network grid over the area to represent the water area available and connected it with the main network (Fig. A2). Animal movement was modelled along this network. To obtain the distribution of step lengths, the distance between any two consecutive tracking locations with the interval of 15 minutes of all animals was calculated with the tool “New Route” in the Network Analyst. For each realized step by an animal, 10 random step lengths were drawn from the respective distribution of all other animals. For each of these step lengths, at least two locations were obtained with a potential forward and backward movement, plus additional locations with sideward movement when watercourses merged or connected to a lake. The exact locations for all potential endpoints with a fixed step length were calculated with the tool “Service Area” in Network Analyst. From this pool of potential steps with the same step length one was randomly chosen to be included in the data. This resulted in 10 control steps with each of differing length, representing what was available to the animal when moving (Fig. A3). As this is a matched case-control design, it was analysed with a conditional logistic regression model (Hosmer & Lemeshow 2004).

To obtain population-level parameter estimates, a two-stage modelling approach (Fieberg *et al.* 2010) was used by employing automated routines that were provided by the `Ts.estim()` function from the R-package `TwoStepCLogit` (Craiu *et al.* 2011). Deviance residuals for each stratum (i.e., each set of one used with ten available points) from the regression were then checked for autocorrelation, following the protocol in Appendix C in Forester et al. (2009).

Using the parameter estimates ($\beta_1,...,\beta_n$) from the conditional logistic model, a RSF that estimates the preference of a habitat depending on the predictor covariates $x= x_1, \ldots, x_n$, can be obtained by

$$RSF(x) = w(x) = \exp(\beta_1 x_1 + \ldots. + \beta_n x_n).$$

.

For any values of the covariates *x*, w(x) represents the RSF score that approximates the respective proportion between the used and the available frequencies (Johnson *et al.* 2008). Values of $w(x)>1$ thus indicate that habitats were over-proportionally selected by the animal with respect to their availability, while $w(x)<1$ represents habitats that were avoided.

To assess the interaction between habitat category and river width, we used the fitted model to calculate RSF scores changing with river width for each of the three categories (main discharge, reservoir, residual water) separately, plugging the mean of the remaining covariates into the model. Pointwise 95% confidence intervals of the RSF were obtained by using the estimated variance-covariance matrix $V(\beta)$ of the β-estimates and employing the approach described in Fox (2003, Section 2). The $V(\beta)$ matrix was estimated via a two-stage bootstrap using 200 iterations in total (Efron & Tibshirani 1986).

3. Results

Between May 2010 and March 2012, 10 otters (three males and seven females) were captured and equipped with implanted transmitters. Nine of them could be tracked for more than six months and were included in the analyses (mean duration in days = 658, min = 252, max = 1032). Combined, the individuals were tracked 13’525 times (mean = 1502, min = 617, max = 2953), with every individual tracked on average 54 times per month (SD ± 12, Table A1).

3.1 Habitat selection at population scale

The MCP for all individuals combined covered an area of 929 km^2, consisting of the habitats main rivers (196 km, 500 ha water surface) and tributaries (1’483 km, 313 ha; Fig. 1). When only water area was considered as available to the animals, all individuals used main rivers most of the time (97.5% of all locations) and only occasionally tributaries (345 locations, 2.5%) during their active periods. They showed no sex-specific difference but overall a significant habitat selection of main rivers (HS-Index=99.99, 95% CI=99.97-99.99).

3.2 Habitat selection at home range scale

Individual home ranges entered the analysis as available area. They were calculated using 10'562 locations (mean ± SD per animal = 1173 ± 550, Fig. A4). The 95% fixed kernels converged at a relative high bandwidth (h = 700) due to the linearity of the freshwater system. Home range size varied between the two estimators with mean river lengths of 85.1 km (± 27.5 SD) in kernels and 32.2 km (± 11.8 SD) in local convex hulls. While the length of the main riverbed with the abstracted water and standing water were consistent between the two estimators at approximately 20 km (T-statistic = -0.1335, p = 0.89), the main difference of river length between the estimators was due to the inclusion of tributaries by the kernel estimator: kernels = 65.0 km, LocoH = 11.6 km (T-statistic = 5.8, p<0.001, Fig. A5). Home range size in males was approximately a third larger compared to the females (kernel: F = 16.1 ± 3.4 km, M = 28.3 ± 2.9 km; LocoH: F = 18.3 ± 6.1 km, M = 25.2 ± 4.1 km). Females had distinct boundaries between them but overlapped with home ranges of the males. Contrary to the expectation that females would select for the most pristine and remote habitat, they also had home ranges in large rivers (N = 2). Both estimators yielded similar results for habitat selection (mean number of independent locations used per animal = 109 ± 39). Logistic regression with standing water as reference category showed a positive selection of the main riverbed (estimate = 1.68 ± 0.30) and a negative selection of tributaries (estimate = -0.89 ± 0.34, both p<0.0001) while the use of abstracted water was indifferent (estimate = 0.45 ± 0.42, Fig. A6). For small scale habitat selection, we focused on the main riverbed as this was positively selected and holds a high diversity in functions.

3.3 Foraging habitat selection within home range

In the two-step conditional logistic regression analyses, all variables that were available to all individuals were included (see Table 1c). The autocorrelation values of the residuals were mostly found to be within 95% confidence bands around zero, indicating no interference by autocorrelation. Foraging habitat selection in the main riverbed appears to be influenced by distance to roads (a proxy for disturbance) and by the river width in dependence on the function of the main riverbed (Table 2, Fig. 2). Animals preferred foraging at a greater distance to roads. In streams up to a width of 12m, reservoirs were highly preferred over main discharge and residual waters. Once the river enlarged, reservoirs were avoided (w(x)<1), while the preference for stretches with main discharge and residual waters increased (w(x)>1). The confidence intervals for main discharge are well above unity for rivers more than 12m, indicating a clear selection of main discharge, given that the watercourse is broad enough.

4. Discussion

Our results show that otters cope surprising well within the human-modified landscape of the Alpine valleys. At three different scales (population, home range and within home range) otters preferred the main riverbed to remote tributaries and standing water. This highlights the importance of the main riverbed as key habitat for otters. However, contrary to our predictions, the studied otters did not show a preference for pristine sections within the main riverbed at the fine scale. Instead, they exploited heavily modified stretches and seemed well adapted to the altered landscape. This study provides evidence on foraging habitat selection of otters, supporting the results of the studies on prey selection by otters in human dominated landscapes (Kloskowski, Rechulicz & Jarzynowa 2013; Pedroso, Marques & Santos-Reis 2014). These results show a flexible habitat selection of a threatened mammal and give a promising perspective for the recovery potential in the Alps by the expanding otter population. Our findings are also encouraging for many other areas with indications of recovering otter populations.

4.1 Effect of fish distribution on foraging habitat selection

The importance of the main riverbeds in foraging habitat selection of otters can most likely be attributed to fish abundance (Clavero, Prenda & Delibes 2003). All of the radiotracked otters placed their home ranges along main riverbeds with a width of more than four meters but avoided the extensive network of tributaries. Otters have been shown to prefer hunting in small streams (e.g. Durbin 1996) which is well explained as fish biomass is negatively correlated to river width (Schager & Peter 2001). However, the negative selection of smaller streams and tributaries of otters in the Alps mirrors the state of these smaller waters: A substantial part of the tributaries are continuous or seasonal torrents, which are heavily modified for flood hazards (Merwald 1986). The alterations disconnect those streams from the main rivers and reduce thus fish abundance.
Conversely, the change of the natural discharge of a river or stream to reservoirs and residual waters should have a negative impact on the habitat selection of otters as fish abundance is expected to be higher in natural stretches of rivers (Fette *et al.* 2007). River bank modifications, vegetation type and width, presence of algae and wood debris are used to identify good fish habitats (BUWAL 1998) and were therefore used here as indicators for

suitable otter habitat. Contrary to our expectations, otters living in a mosaic of altered and natural stretches of watercourses select for the modified parts.

We believe that a key reason for the preference for reservoirs is due to the unintentional food supply provided by humans. In the study area, fishing associations and private persons rent stretches of running fish waters (varying from <1 km to 10 km), where they stock fish (usually salmonid species) at any time of the year. At the release site, the increase of the fish biomass can be short-lived: stocked fish often disperse quickly downstream due to antagonistic behaviour of the resident conspecifics, low foraging efficiency, reduced stamina and a general habitat preference for open water (Weiss & Schmutz 1999; Weber & Fausch 2003). The strong current in streams (width <12m) may favour the downstream movement of hatchery-reared fish to the next reservoir. Often large shoals of fish could be observed few days after stocking events occurred upstream in the study area (I. Weinberger, pers. observation). The regime of fish stocking can thus temporarily change a prey-depleted reservoir into a rich foraging ground. Such aggregations of fish were not observed in the reservoirs of the wide rivers, possibly because stocked fish adapts more easily to the lower current of these rivers or because otters prefer to hunt in shallow waters at 0-3m depth (Nolet, Wansink & Kruuk 1993). This would explain the negative habitat selection of reservoirs in large rivers (width >12m).

The selection for the residual waters is inversed to the selection of dam reservoir. Residual water is avoided when the river width is <12m but becomes strongly selected when wider. This is likely due to the amount of water discharge after the dam. In streams, the effect of water loss in the main riverbed is more pronounced than in rivers. Residual waters of large rivers may carry enough water in the meantime to sustain several fish species and therefore harbour more prey than streams.

Surprisingly, standing waters were negatively selected. Particularly fishponds harbour a higher fish biomass per area than the main river. Otters are known to be very attracted to fishponds (Kranz 2000), a common source of human-wildlife conflicts. There were at least 120 managed fishponds in the study area, with many of them not effectively protected against otter intrusion. It was unexpected to see that none was regularly visited by the studied otters. This indicates that food availability and accessibility within the watercourses is high enough for otters to sustain themselves. However, if prey density is decreasing, otters may rely more on unprotected fishponds. Thus, this endangered carnivore exhibits a behavioural plasticity in habitat use not uncommon in other carnivore species (Contesse *et al.* 2004; Moss, Alldredge & Pauli 2015).

4.2 Effect of human disturbance on otter habitat selection

Otters used the complete range from pristine streams to heavily modified large rivers. Contrary to the hypothesis that females choose more remote areas than males, the radio-tracked females were found in watercourses of all widths, with varying degrees of modification and human disturbance. However, the three females successfully rearing young had their territories in medium-sized streams (4-10m width). Reproductive success may indeed be higher in less disturbed habitat, either due to a higher food availability, lower human disturbance or an avoidance of predation by conspecific males (Balme *et al.* 2013). Human disturbance, expressed by distance to paved roads, played a more significant role than in other tracking studies (e.g. Durbin, 1998; Green et al., 1984). For foraging, otters chose the areas, where human disturbance was the lowest within their home ranges.
This is in accordance with other studies on carnivores, where human disturbance has been shown to shape behavioural patterns, e.g. red fox, cougar or lynx (Bouyer *et al.* 2015; Díaz-Ruiz *et al.* 2015; Smith *et al.* 2015).
Although the inference from a few radiotracked individuals needs to be treated cautiously, we are confident that the observed impact of human disturbance might be even more pronounced in situations with higher human pressure.

5. Conclusions and management implications

This study demonstrates that the endangered otter is among the carnivore species that appear to adapt to modified habitat and persist in human-dominated landscapes. This species copes well within semi-natural watercourses interspersed by a multitude of barriers and infrastructure for risk management and energy production. We showed that individual otters actually prefer to forage in highly modified habitats such as reservoirs and residual waters while they keep distance to human disturbance. This flexible foraging habitat selection may be the corner stone of otter expansion, particularly to areas with low disturbance by humans. Our results are highly promising for the recovery of the otter in the modern landscape of the Alps and Western Europe.
However, habitat requirements for foraging animals are strongly associated with the availability and accessibility to their main prey. Humans often alter prey abundance by husbandry and thus influence resource use by carnivores. The current regime of fish stocking seems beneficial to otter presence but, at the same time, reinforces the risk of human-wildlife conflicts. Our results suggest that as long as abundant prey is available, otters are highly tolerant of even strong modifications to their aquatic habitat. We suspect that fish stocking could be a crucial prerequisite for part of the observed preferences and may even act as a fragile driver for the current geographic re-expansion of the species.

However, otter densities in streams appear unaffected by stocking regime (Sittenthaler *et al.* 2015). Alternatively, the availability of resting sites may be another limiting factor for otter distribution in a human-dominated landscape as shown in other mustelid species (Manning *et al.* 2013) and needs to be explored. Contemporary efforts to restore rivers and streams may improve habitat quality and foster, in the medium term, otter recovery. Our result demonstrate that it is crucial to understand how the interplay of hydropower infrastructure and fish stocking regime influences the natural resources of predators and prey in order to manage and mitigate human-wildlife conflicts.

Acknowledgements

This study was organised by the foundation Pro Lutra, Switzerland and funded by Zuercher Tierschutz, Ernst Goehner Stiftung, Stotzer-Kaestli-Stiftung, Bernd Thies-Stiftung, Autax-Stiftung, Stiftung Temperatio, Conseil International de la Chasse CIC – Sektion Schweiz, Theo-Wucher Stiftung, Claraz-Schenkung, Charlotte und Nelly Dornacher Stiftung, Peter and Anna Weinberger and an anonymous sponsor. Environmental data was provided by GIS Steiermark (Divison 7). Authorization for capture and treatment of otters was given by the government of Styria, Austria (Division 10a and 13c).
We thank Tjibbe de Jong and Lena de Jongh for help capturing the animals and the veterinarians Ivanna Antos, Christa Weissenbacher and Gerd Kaltenegger for conducting the surgeries. We are much indebted to Susana Freire, Iris Hanetseder, Barbara Schnueriger, André Weller, Susanne Pusch, Yves Schwyzer, Gašpar Camlik, Vašek Beran, Lukas Poledník, Aleš Toman, Anja Roy and Manuel Freiburghaus for their fieldwork. Two anonymous reviewers contributed substantially to the manuscript. Finally, we are thankful for the discussions and inputs: Tobias Roth, John Fieberg, Benedikt Gehr, Mirco Lauper, Patrick Laube and Alex van Rensburg.

References

Bain, M.B., Finn, J.T. & Booke, H.E. (1988) Streamflow Regulation and Fish Community Structure. *Ecology*, **69**, 382–392.

Balme, G.A., Batchelor, A., De Woronin Britz, N., Seymour, G., Grover, M., Hes, L., Macdonald, D.W. & Hunter, L.T.B. (2013) Reproductive success of female leopards Panthera pardus: The importance of top-down processes. *Mammal Review*, **43**, 221–237.

Bifolchi, A. & Lode, T. (2005) Efficiency of conservation shortcuts: An investigation with otters as umbrella species. *Biological Conservation*, **126**, 523–527.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R.C., Odden, J. & Linnell, J.D.C. (2015) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Animal Conservation*, **18**, 271–278.

Bueno-Enciso, J., Diaz-Ruiz, F., Almeida, D. & Perreras, P. (2014) Effects of flow regulation and non-native species on feeding habits of Eurasian otter Lutra Lutra in mediterranean temporary rivers. *River Research and Applications*, **30**, 1296–1308.

BUWAL. (1998) *Ökomorphologie Stufe F - Methoden zur Untersuchung und Beurteilung der Fliessgewässer der Schweiz*. Bern.

Calenge, C. (2006) The package 'adehabitat' for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V. & Adamec, M. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**, 1517–1519.

Clavero, M., Prenda, J. & Delibes, M. (2003) Trophic diversity of the otter (Lutra lutra L.) in temperate and Mediterranean freshwater habitats. *Journal of Biogeography*, **30**, 761–769.

Comiti, F. (2012) How natural are Alpine mountain rivers? Evidence from the Italian Alps. *Earth Surface Processes and Landforms*, **37**, 693–707.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004) The diet of urban foxes (Vulpes vulpes) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology - Zeitschrift fur Saugetierkunde*, **69**, 81–95.

Craiu, R. V., Duchesne, T., Fortin, D. & Baillargeon, S. (2011) Conditional Logistic Regression With Longitudinal Follow-up and Individual-Level Random Coefficients: A Stable and Efficient Two-Step Estimation Method. *Journal of Computational and Graphical Statistics*, **20**, 767–784.

Díaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B. & Ferreras, P. (2015) Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? *Journal of Zoology*, **298**, 128-138

Durbin, L.S. (1996) Individual differences in spatial utilization of a river-system by otters Lutra lutra. *Acta Theriologica*, **41**, 137–147.

Durbin, L.S. (1998) Habitat selection by five otters Lutra lutra in rivers of northern Scotland. *Journal of Zoology London*, **245**, 85–92.

Efron, B. & Tibshirani, R. (1986) Bootstrap Methods for Standard Errors, Confidence Intervals, and Others Measures of Statistical Accuracy. *Statistical Science*, **1**, 54–77.

Elmeros, M., Hammershøj, M., Madsen, A.B. & Sogaard, B. (2006) Recovery of the otter

Lutra lutra in Denmark monitored by field surveys and collection of carcasses. *Hysterix*, **17**, 17–28.

ESRI. (2011) ArcGIS Desktop: Release 10.

ESRI. (2002) ArcView: Release 3.2

Ferna, R. (1998) Changes in otter Lutra lutra distribution in Central Spain in the 1964 ± 1995 period. *Biological Conservation*, **86**.

Fette, M., Weber, C., Peter, A. & Wehrli, B. (2007) Hydropower production and river rehabilitation: A case study on an alpine river. *Environmental Modeling and Assessment*, **12**, 257–267.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010) Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2233–44.

Forester, J.D., Im, H.K. & Rathouz, P.J. (2009) Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*, **90**, 3554–65.

Fortin, D., Beyer, H., Boyce, M. & Smith, D. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Foster-Turley, P., Macdonald, S.M. & Mason, C.F. (1990) *Otters: An Action Plan for Their Conservation*. IUCN Otter Specialist Group.

Fox, J. (2003) Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software*, **8**, 1–27.

Green, J., Green, R. & Jefferies, D. (1984) A radio-tracking survey of otters Lutra lutra on a Perthshire river system. *Lutra*, **27**, 86–145.

Hafs, A.W., Harrison, L.R., Utz, R.M. & Dunne, T. (2014) Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. *Ecological Modelling*, **285**, 30–38.

Hosmer, D.W. & Lemeshow, S. (2004) *Applied Logistic Regression*. Wiley, New York.

Jacobs, J. (1974) Quantitative Measurement of Food Selection: A Modification of the Forage Ratio and Ivlev’s Electrivity Index. *Oecologia*, **14**, 413–417.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Johnson, D.S., Thomas, D.L., Hoef, J.M. Ver, Christ, A., Service, F. & Ver Hoef, J.M. (2008) A general framework for the analysis of animal resource selection from telemetry data. *Biometrics*, **64**, 968–76.

Juhász, K., Lukács, B.A., Perpék, M., Nagy, S.A. & Végvári, Z. (2013) Effects of extensive fishpond management and human disturbance factors on Eurasian otter (Lutra lutra L. 1758) populations in Eastern Europe. *North-Western Journal of Zoology*, **9**, 227–238.

Kloskowski, J., Rechulicz, J. & Jarzynowa, B. (2013) Resource availability and use by Eurasian otters Lutra lutra in a heavily modified river-canal system. *Wildlife Biology*, **19**, 439–451.

Knopff, A.A., Knopff, K.H., Boyce, M.S. & St. Clair, C.C. (2014) Flexible habitat selection by cougars in response to anthropogenic development. *Biological Conservation*, **178**, 136–145.

Kranz, A. (2000) Otters (Lutra lutra) increasing in Central Europe: From the threat of extinction to locally perceived overpopulation? *Mammalia*, **64**, 357–368.

Kranz, A. & Polednik, L. (2015) *Fischotter in Kaernten: Verbreitung & Bestand 2014.* Endbericht im Auftrag des Amtes der Kaerntner Landesregierung. Graz.

Kranz, A. & Poledník, L. (2012) *Fischotter Verbreitung und Erhaltungszustand*. Endbericht. Graz.

Kranz, A., Polednik, L., Pavanello, M. & Kranz, I. (2013) Fischotterbestand in der Steiermark - Spurschneekartierungen 2010 - 2013*.* Endbericht. Graz.

Kranz, A. & Toman, A. (2000) Otters recovering in man-made habitats in central Europe. *Mustelids in a modern world*, (ed H.I. Griffiths), pp. 163–184. Bachhuys Publishers, Leiden, Netherlands.

Krawczyk, A.J., Bogdziewicz, M., Majkowska, K. & Glazaczow, A. (2016) Diet composition of the Eurasian otter Lutra lutra in different freshwater habitats of temperate Europe: a review and meta-analysis. *Mammal Review*.

Kruuk, H. (1995) *Wild Otters: Predation and Populations*. Oxford University Press Inc., Oxford UK.

Kruuk, H. (2006) *Otters: Ecology, Behavious and Conservation*. Oxford University Press Inc., Oxford UK.

Lyons, A., Turner, W. & Getz, W. (2013) Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology*, 1:2

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Seletion by Animals*, 2nd Editio. Kluwer Academic Publishers, Dordrecht, Netherlands.

Manning, A.D., Gibbons, P., Fischer, J., Oliver, D.L. & Lindenmayer, D.B. (2013) Hollow futures? Tree decline, lag effects and hollow-dependent species. *Animal Conservation*, **16**, 395–403.

Merwald, I.E. (1986) Wildbäche als Fischgewässer. *Österreichs Fischerei*, **39**, 293–305.

Moss, W.E., Alldredge, M.W. & Pauli, J.N. (2015) Quantifying risk and resource use for a large carnivore in an expanding urban-wildland interface. *Journal of Applied Ecology*.

53, 371-378

Naiman, R., Decamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological applications*, **3**, 209–212.

Nolet, B. a., Wansink, D.E.H. & Kruuk, H. (1993) Diving of otters (Lutra lutra) in a marine habitat: use of depths by a single-prey loader. *Journal of Animal Ecology*, **62**, 22–32.

Ó Néill, L., de Jongh, A., Ozoliņš, J., Jong, T. De & Rochford, J. (2007) Minimizing Leg-Hold Trapping Trauma for Otters With Mobile Phone Technology. *Journal of Wildlife Management*, **71**, 2776–2780.

Pedroso, N.M., Marques, T. a. & Santos-Reis, M. (2014) The response of otters to environmental changes imposed by the construction of large dams. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **24**, 66–80.

Prenda, J., Lopez-Nieves, P. & Bravo, R. (2001) Conservation of otter (Lutra lutra) in a Mediterranean area: the importance of habitat quality and temporal variation in water availability. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **11**, 343 – 355.

Prigioni, C., Balestrieri, A. & Remonti, L. (2007) Decline and recovery in otter Lutra lutra populations in Italy. *Mammal Review*, **37**, 71–79.

R Development Core Team (2015) A language and environment for statistical computing. R Foundation for Statistical Computing.

Ramesh, T., Kalle, R. & Downs, C.T. (2015) Sex-specific indicators of landscape use by servals: Consequences of living in fragmented landscapes. *Ecological Indicators*, **52**, 8–15.

Reid, N., Thompson, D., Hayden, B., Marnell, F. & Montgomery, W.I. (2013) Review and quantitative meta-analysis of diet suggests the Eurasian otter (Lutra lutra) is likely to be a poor bioindicator. *Ecological Indicators*, **26**, 5–13.

Ripple, W.J., Estes, J. a, Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343.**

Roos, A., Loy, A., de Silva, A., Hajkova, P. & Zemanová, B. (2015) Lutra lutra. The IUCN Red List of Threatened Species 2015, http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T12419A21935287.en

Sales-Luís, T., Pedroso, N.M. & Santos-Reis, M. (2007) Prey availability and diet of the Eurasian otter (Lutra lutra) on a large reservoir and associated tributaries. *Canadian Journal of Zoology*, **85**, 1125–1135.

Schager, E. & Peter, A. (2001) *Bachforellensoemmerlinge*. Kastanienbaum, Schweiz.

Sittenthaler, M., Bayerl, H., Unfer, G., Kuehn, R. & Parz-Gollner, R. (2015) Impact of fish stocking on Eurasian otter (Lutra lutra) densities: A case study on two salmonid streams

Author: *Mammalian Biology*, **80**, 106–113.

Smith, J.A., Wang, Y., Wilmers, C.C. & Smith, J.A. (2015) Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B*, **282**.

Stöcklin, J., Bosshard, A., Klaus, G., Rudmann-Maurer, K. & Fischer, M. (2007) *Synthesebericht NFP 48 Landnutzung Und Biologische Vielfalt in Den Alpen*.

Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014) Applications of step-selection functions in ecology and conservation. *Movement Ecology*, **2**.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.

Weber, J.-M. (2011) Food habits of escaped Eurasian otters (Lutra lutra) in a suburban environment in Switzerland. *Revue Suisse de Zoologie*, **118**, 485–489.

Weber, E.D. & Fausch, K.D. (2003) Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1018–1036.

Weiss, S. & Schmutz, S. (1999) Response of resident brown trout, Salmo trutta L., and rainbow trout, Oncorhynchus mykiss (Walbaum), to the stocking of hatchery-reared brown trout. *Fisheries Management and Ecology*, **6**, 365–375.

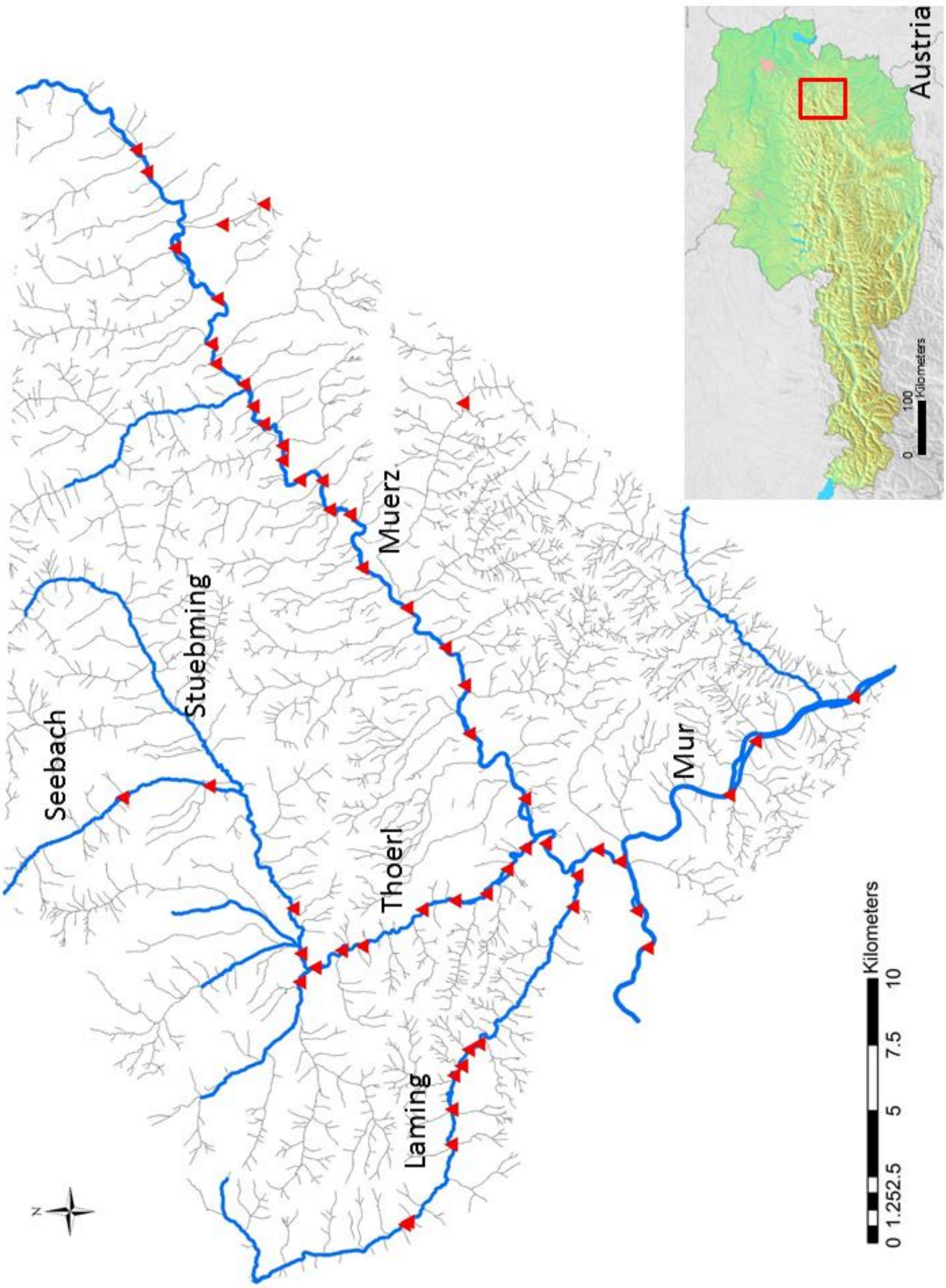


Fig. 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters showing the running and standing water bodies. Blue = watercourses ≥4m, grey= streams <4m. Red triangles=reservoir dams (n=55).

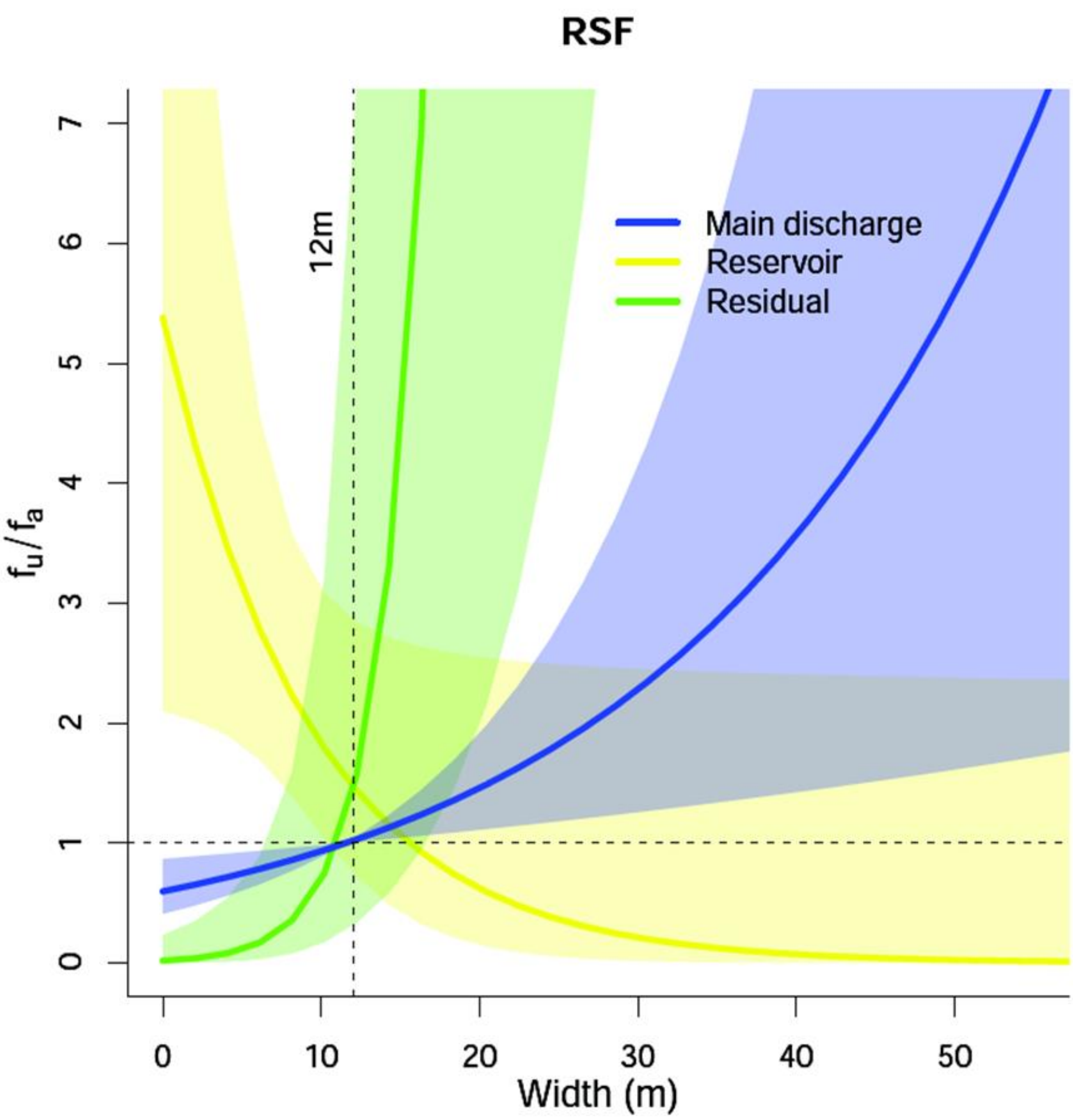


Fig. 2. Resource selection function (RSF) changing with width conditionally on each of the three habitat functions of the main riverbed (main discharge, reservoir and residual).The proportion f_u / f_a relatesused and available frequencies. Shaded areas encompass all pointwise 95% confidence intervals.

Table 1. Variables used for habitat selection analysis at three spatial scales

Variables		**Description**	**Measurement** [unit]
a) Population level			
River width		<4m or ≥4m	Categorical
b) Home range level			
Habitat type	Main riverbed	Original riverbed	Categorical
	Abstracted water	Water diverted from the reservoir to the hydropower plant (power plant channel) and back to the main riverbed (downstream water outlet)	Categorical
	Standing water	Lakes, ponds and fishponds	Categorical
	Tributary	All small streams flowing in the main rivers	Categorical
c) Within home range level			
Function of the main riverbed	Main discharge	Unhindered flow of all discharge within the main riverbed	Categorical
	Reservoir	Slow moving water above the dam, sandy and deeper bottom	Categorical
	Residual water	Regulated flow below the dam until tail water from hydroelectric power station joins	Categorical
River width		Main riverbed width	Continous [m]
Depth		Variability of water depth within the river	Ordinal (1-3, with 1= large, 3=no variability)
River bank modification		Alterations and bank reinforcement	Ordinal (1-5, with 1= none, 5=completely altered)
Vegetation width		Width of natural or semi-natural vegetation measured from waterside	Continous [m]
Vegetation type		Type of vegetation from the river perspective: “natural” (forest, reed, herbaceous stretches with at least 1 tree/bush within 25m), “foreign” (herbaceous, meadow, grass), “artificial” (none)	Ordinal
Algae		Estimated amount of Algae in river- bed	Ordinal (from 1=none to 3=exceeding)
Wood debris		Wood washed up at the bankside	Ordinal (from 1=heaps to 3=none/little)
Distance to fishponds		Known fishponds within home ranges	Continous [m]
Distance to dams		Dams for hydropower plant	[m]
Distance to roads		Paved roads	[m]

Table 2. Two-step conditional logit over all nine animals. Significant factors are bold.

Covariates	Beta	SD	p-value (Wald)
Distance to road	**0.063**	**0.031**	**0.020**
FUNCTION OF RIVERBED : WIDTH (main discharge as reference category)			
Residual water : width (p=0.0.27)	**3.115**	**1.621**	
Reservoir : width (p=0.035)	**-2.036**	**1.126**	
Distance to dam	-0.103	0.077	0.090
River width	0.599	0.45	0.092
Algae	0.057	0.058	0.162
Distance to fishpond	-0.098	0.101	0.166
Type riparian vegetation	-0.035	0.041	0.194
Width riparian vegetation	-0.038	0.073	0.303
FUNCTION OF RIVERBED (main discharge as reference category)			
Reservoir	0.207	0.515	0.344
Residual water	0.288	1.285	0.411
Wood debris	0.027	0.086	0.377
Riverbank modifications	-0.002	0.038	0.474
Variability in depth	-0.002	0.054	0.483
Material bank side	0.000	0.033	0.500

Supplementary Material

Table A1. Summary of the nine otters tracked and included in the analyses

Animal	Sex	Age at Capture	Start Tracking	Reason for End	Tracking Duration (Days)	No of fixes	Mean No of fixes/Month
Alena	F	Sub-adult	08/05/2010	Study	1032	2953	72
Baukje	F	Adult	07/11/2010	Study	849	2197	61
Cleo	F	Sub-adult	10/11/2010	Battery life	583	1266	51
Dan	M	Adult	10/11/2010	Study	848	1518	31
Fee	F	Sub-adult	03/05/2011	Study	688	1416	48
Gessa	F	Adult	03/05/2011	Study	685	1295	44
Hans	M	Adult	07/05/2011	Study	672	1320	49
Ivo	M	Adult	14/04/2012	Study	313	943	66
Johanna	F	Adult	14/04/2012	Disappearance	252	617	63

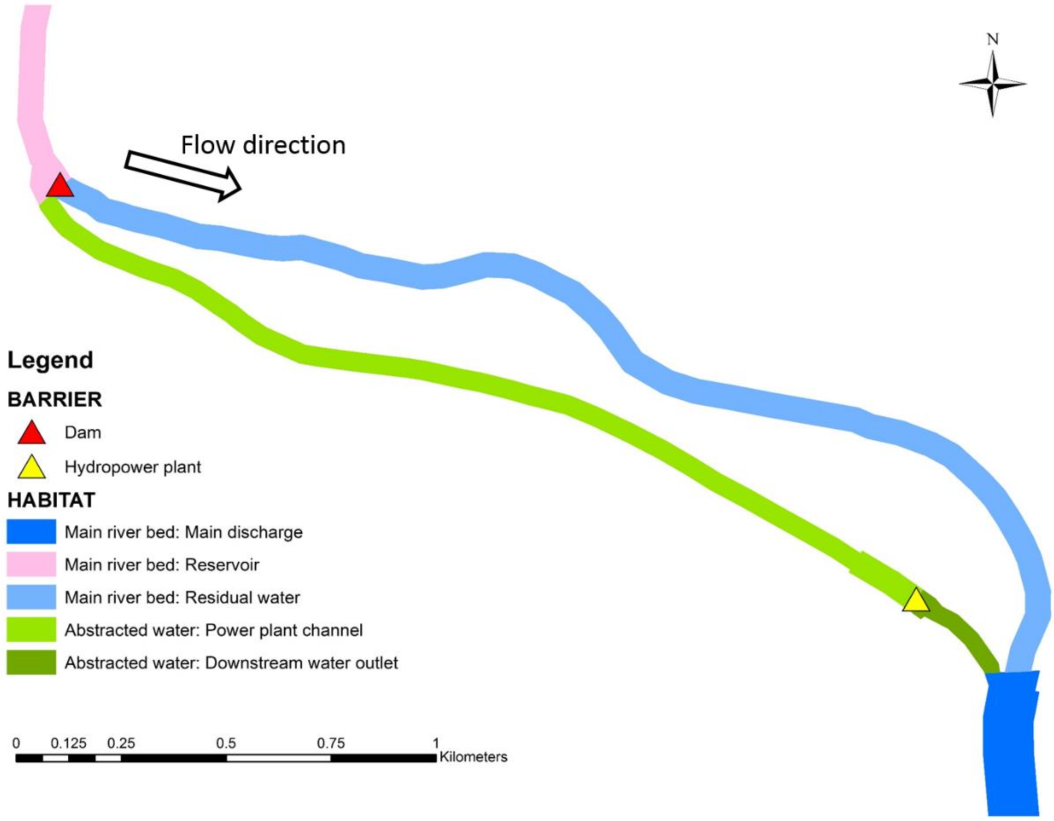


Fig. A1. Schematic drawing of the habitat category types of watercourses, except tributaries.

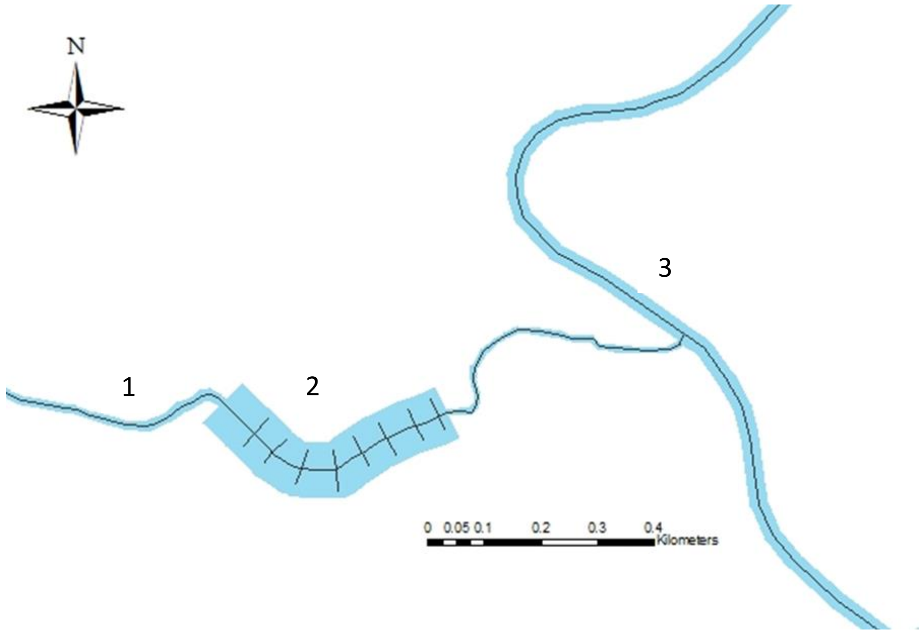


Fig. A2. Schematic setup of river network in GIS. River network with the river width (blue coloured): a stream (1) flows into a reservoir (2) and then into a larger river (3). The river network in ArcGIS is the black line. As the reservoir is several times wider than the stream, a grid has been laid over the single network line in order to mirror availability of this habitat.

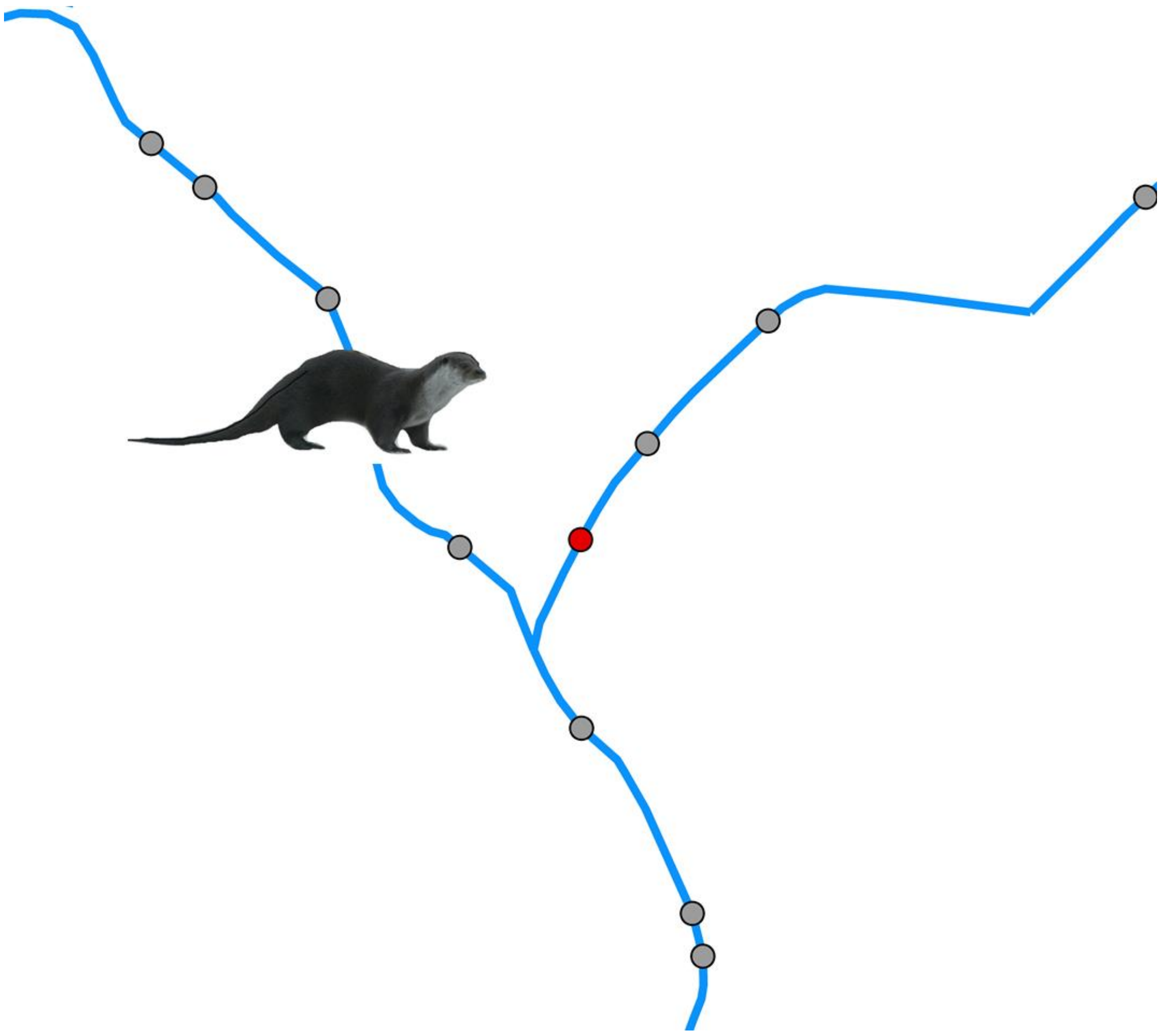
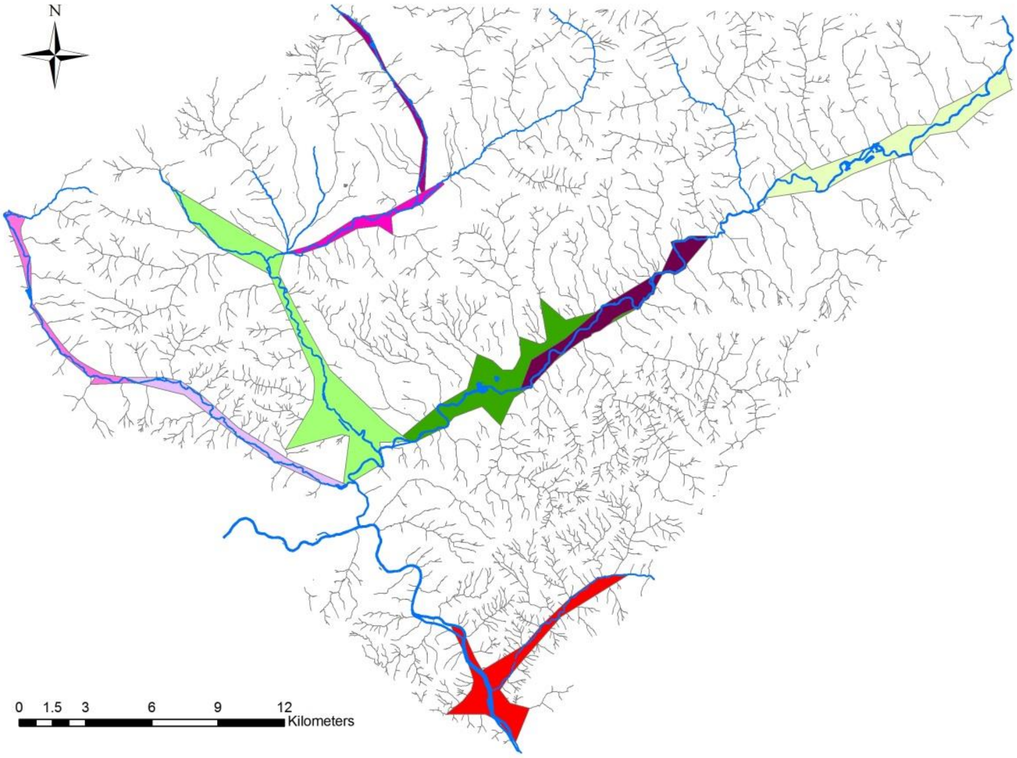


Fig. A3. In a step selection function, for any given step an individual takes, random steps are drawn from two distributions (angles and lengths) of angles and steps of other individuals of the same population (Thurfjell et al. 2014).
The end location of a real step (red point) is compared to the random steps of differing lengths (grey points) from the same (real) starting location (otter). As the distribution of the angles is inherently given by the linear system, only the distribution of step lengths was used.



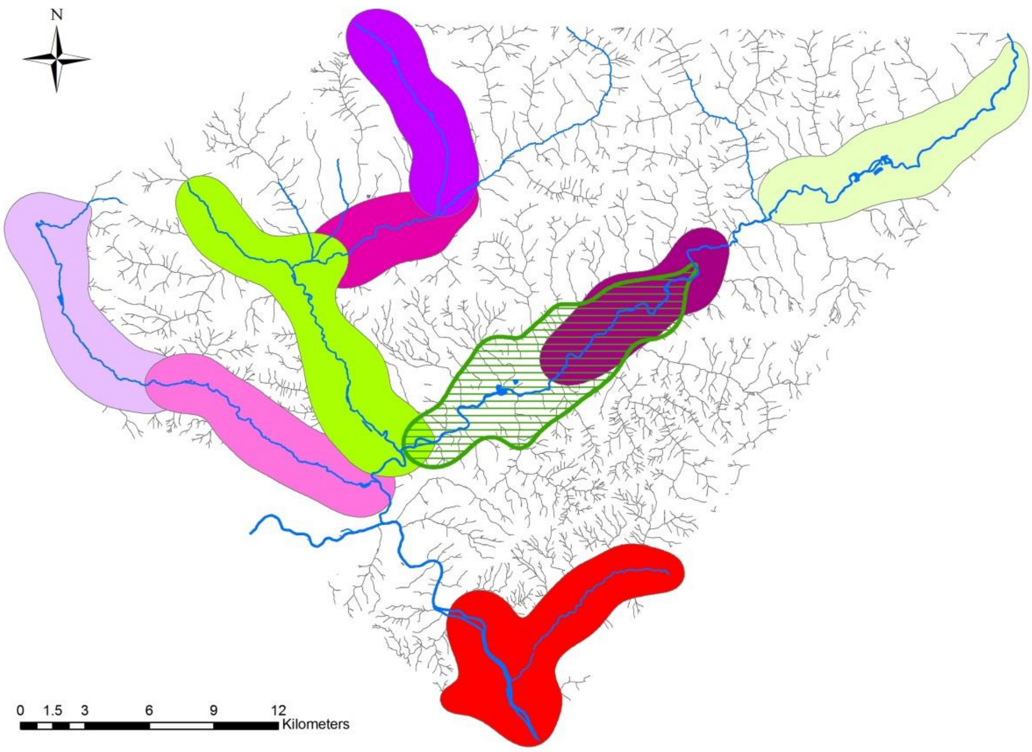


Fig. A4. Estimation of continuous home ranges with two different methods: Local convex hull (upper) and fixed kernel (below). Female home ranges are in shades of red/blue, male home ranges in green.

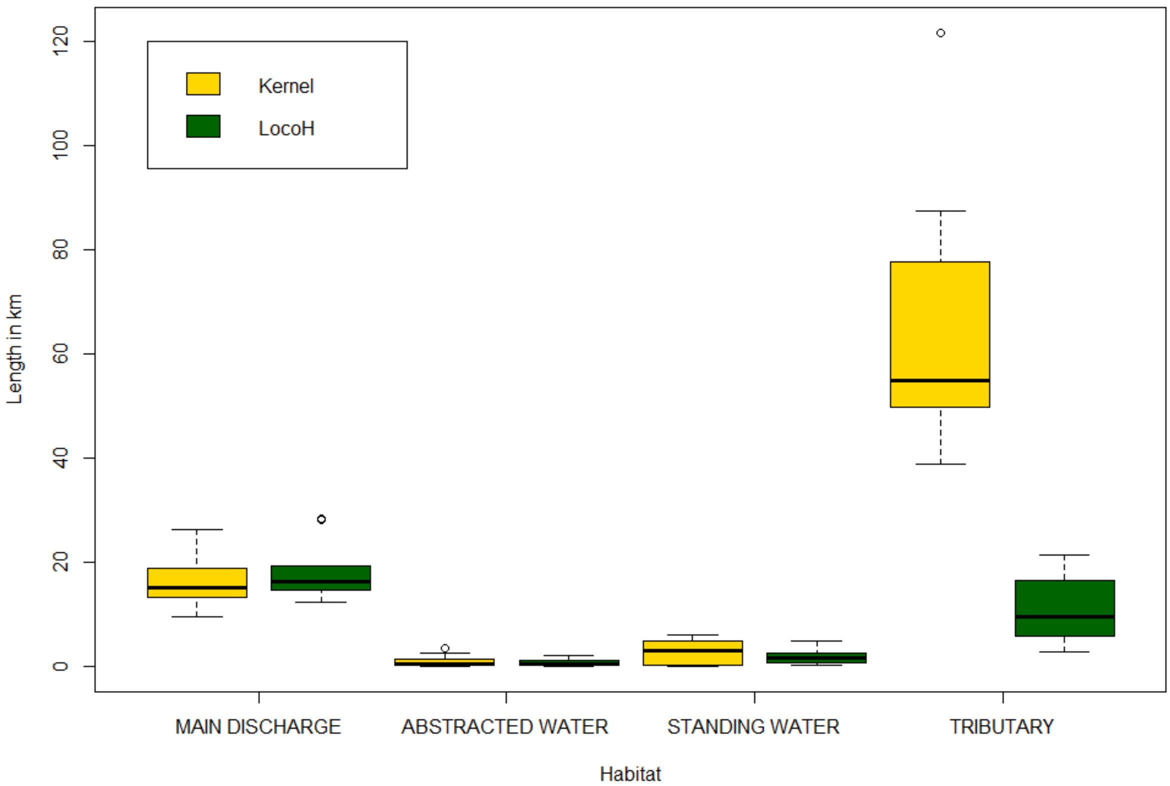


Fig. A5. Difference in length between 95% fixed kernel and 95% LocoH for the four main habitat categories. Only the length of tributaries is larger in the home ranges using the Kernel estimator than using LocoH.

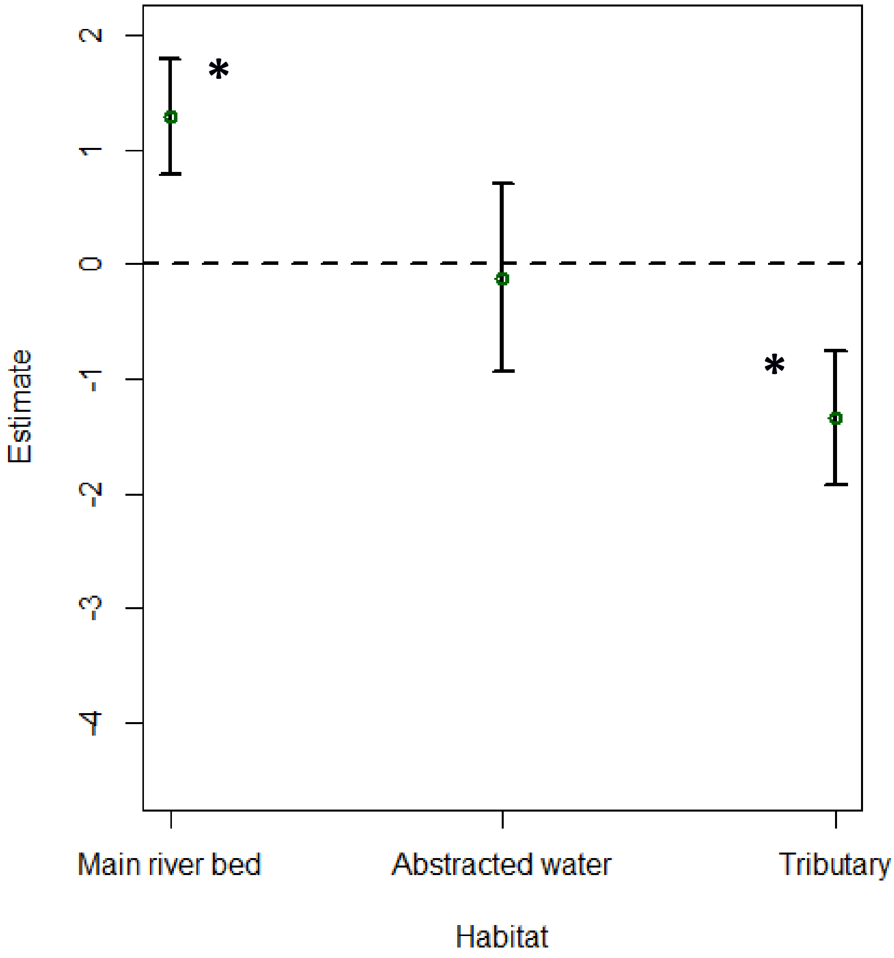


Fig. A6. Active locations of animals in the categories main riverbed, abstracted water and tributary compared to standing waters (ponds). Asterisk indicate significant deviation from standing water

Chapter 3

Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape

Irene C. Weinberger, Stefanie Muff, Andreas Kranz & Fabio Bontadina

(Ready for submission to Animal Conservation)

Loss of riparian vegetation and increasing human presence alter the riverine landscape

Abstract

In many humanized landscapes, the riparian vegetation belt is one of the few remaining cover structures for wildlife. However, the natural riparian landscapes, being continuously modified for humans, are also under growing pressure of leisure activities. Humans cause disturbances to wild animals that can surpass natural predation risk. As resting sites are important shelters to avoid predation, human disturbance could strongly shape resting site selection.

To test the impact of perceived predation risk, we investigated the effect of human presence on resting site selection of otters. In freshwater systems, the otter rests during the day in close proximity to waterbodies. However, undisturbed belts of natural riparian vegetation are scarce in Europe due to modifications of the watercourses, intensive network of roads and farming practices. We equipped nine otters with transmitters and analysed daily resting site selection and location of the resting sites in relation to human disturbances at different scales up to 30 months.

Altogether, we identified 285 unique resting sites. Most of them were exclusively found in riparian vegetation (95%), where natural riparian vegetation was highly preferred compared to altered or no vegetation. There is strong evidence that human disturbance influenced resting site selection with the consequence that with increasing disturbance level, the animals preferred areas with a wider riparian vegetation width.

Our results suggest that otters indeed choose their resting sites depending on the human disturbance during the day. They avoid locations where humans could be expected to disrupt their rest. An intact riparian vegetation belt provides protection from human disturbance in areas where human presence in the immediate surroundings is high. Otter can thus cope living in regions with high human pressure given safe refuges to rest. Our study stresses the relevance of a natural and wide riparian vegetation belt for wildlife in an otherwise depleted landscape.

Key words

Riparian vegetation, resting site selection, Lutra lutra, Eurasian otter, Human disturbance, Alps, conservation, riverine landscape, radiotracking

Introduction

Fear is an important component in habitat selection (Brown, Laundre & Gurung 1999). Animals try to minimize predation risk by altering the behaviour or time allocation patterns (Laundré, Hernández & Ripple 2010). Human-induced disturbances are analogous to predation risk, resulting in declines in fitness and abundance of wildlife populations (Frid & Dill 2002). Indeed, human disturbance is one of the driving factors for species distribution (Murphy & Romanuk 2014). The impact of human activities actually exceeds the behavioural response to natural predators (Ciuti *et al.* 2012). This is of growing concern as the human population increases steadily (Coetzee & Chown 2015).

One of the most vulnerable states for any animal is sleeping, during which it is subject to unfavourable biotic and abiotic factors (Reichman & Smith 1990). While sleeping, animals are sensitive to the predation risk and apply tactics like hiding in a safe place or forming groups (see Semeniuk & Dill 2005). Not only prey species but also carnivores shift to safe habitats to rest (Oriol-Cotterill *et al.* 2015; Llaneza *et al.* 2016). The availability and quality of resting sites can therefore be a limiting factor for the occurrence of any species (Manning *et al.* 2013).

A key component to lower the risk of disturbance is vegetation cover because it decreases the chance of detection (Mysterud & Østbye 1999; Boydston *et al.* 2003). In many humanized landscapes, the riparian vegetation belt is one of the few remaining cover structures for wildlife. Although its importance for biodiversity is known (Bennett, Nimmo & Radford 2014), this type of vegetation has been reduced, converted to agricultural lands or replaced by human settlements (Rey Benayas & Bullock 2015). Additionally, riparian areas are attractive landscapes for human leisure activities (Kienast *et al.* 2012), with natural stretches being preferred (Mccormick, Fisher & Brierley 2015). For semi-aquatic species, the loss of riparian vegetation and a concurrent increase of human activities along the watercourse may pose a serious threat.

The otter is a medium sized semi-aquatic predator, living a nocturnal and elusive life in freshwater systems. In the last century, the species underwent a massive decline caused by habitat fragmentation, persecution and pesticides (Foster-Turley, Macdonald & Mason 1990). Since few decades, a slow recovery of some populations is being observed (e.g. Janssens *et al.* 2006; Prigioni, Balestrieri & Remonti 2007). In recent years, the species is also expanding again into the Alpine Arc (Kranz & Poledník 2012, 2015). There, the landscape has been altered massively in the last 50 years due to an increase of industry, tourism and human population expansion (Comiti 2012). Simultaneously, large parts of the natural riparian vegetation have been lost or degraded to small belts.

Due to their secrete lifestyle, only few studies addressed resting site selection of otters in freshwater systems (e.g. Green, Green & Jefferies 1984; Beja 1996; Durbin 1998). Otters sleep during the day, usually resting within 50 m distance to the nearest water body, with the main part of the resting sites within 10 m to the water front (Green, Green & Jefferies 1984; Beja 1996). It can be thus assumed, that resting sites are usually situated within the stripe of the riparian vegetation along the freshwater system. For otters, two types of resting site structures are used in literature: cavities like the tree root system or boulders (“holts”) and resting site above ground (“couches”) (Green, Green & Jefferies 1984).
The impact of human presence on resting site location of otters is assumed to be weak (Green, Green & Jefferies 1984; Beja 1996). Generally, the reaction of animals to disturbance can vary between different sources of disturbance e.g. presence of roads or pedestrians (see Blanc et al. 2006). Alternatively, the type of human activity or the predictability of human presence may influence the response of the animal. In the Alpine Arc, many anthropogenic structures such as roads are in close proximity to watercourses. A fair amount of hiking and cycling paths exists along the riparian vegetation, which are highly attractive to humans for leisure activities such as jogging, walking or fishing. Those activities could be perceived as potential disturbance by otters, especially if dogs are present (Kruuk 1995; Blanc *et al.* 2006). In industrial zones, human presence is practically permanent, while along hiking paths or on agricultural fields, an encounter with humans remains unpredictable. We assessed resting site selection of otters in relation to riparian habitat and with focus on human disturbance. If otters perceive roads indeed as cause of disturbance, they either should avoid resting in their proximity or prefer vegetation cover as buffer. We therefore predicted according to Blanc et al. (2006) that roads should have a lower effect on resting site selection than pedestrians. Accordingly, we expected that if humans are perceived as threats, then resting sites should be found either in areas with low human presence or where the resting sites are sheltered by vegetation from human disturbance. Alternatively, the structure of the resting site may vary depending on human pressure. We thus expected a preference for underground structures when disturbance is high.

Methods

Study area

The field study was conducted from May 2010 to March 2013 in the eastern Central Alps in Styria, Austria (N47°24’36”, E15°16’7”). The study areacovers approximately 1760 km^2, with about 3090 km length of streams and rivers (Fig. 1). All watercourses belong to the catchment basin of the river Mur (mean annual discharge of approx. 110 m^3/s). The Muerz valley, named after the river Muerz (mean annual discharge of 20 m^3/s), is the main valley in the study area. The elevation of the valley floor ranges from 458 to 974 m, with the surrounding mountains up to 1850 m. Urban areas, intensive agriculture and iron industry dominate the lower valleys. Agriculture, forestry and small settlements contribute to the landscape in the higher valleys. Many stretches of the watercourses are modified or regulated for electrical power exploitation. Often, the riparian vegetation belt has been reduced to a small stripe of one to eight m width, due to infrastructures like roads or buildings or due to farming practices. A large amount of people practice outdoor activities such as jogging, cycling and fishing.

Capture and radiotracking

Captures took place in spring and autumn between 2010 and 2012. Otters were trapped with soft-catch traps (No. 3, Oneida Victor Inc., Cleveland, Ohio) coupled with GSM trap alarms (Ó Néill *et al.* 2007). Within 30 minutes of capture, animals were removed from the traps. After the intraperitoneal implantation of the transmitter (model 325/L, model 400/L, Telonics Inc., Mesa, Arizona) in a vet-ambulance, the animals were released within 24 hours of capture. Animals were tracked up to four times a week between sunrise and sunset spaced out over the day. Tracking was conducted by a single person using a receiver (Sika, Biotrack Ltd, Dorset UK), a handheld 3-element Yagi-antenna and an omnidirectional antenna placed on the car roof. The activity of the animal was deduced from the variation in signal strength and classified into three categories: (1) active, (2) passive and (3) unknown. When passive, the resting site was identified by homing-in to an accuracy of <5m. GPS locations were taken for new resting sites without disturbing the animal. Habitat variables were attributed to the locations using ArcMap 10 (ESRI 2011). Animals were tracked until the transmitter failed, the animal disappeared or the field study ended in March 2013. Data from the first ten days after transmitter surgery and all active data were excluded.

Habitat variables

Environmental parameters of newly identified resting sites were assessed when the animal was absent. The type of resting site was categorized into one of the three following classes: “couch” (above ground, in the vegetation or in a structure such as a stickpile), “holt” (underground) and unknown, when no clear assignment to the other two could be made. The type of water body within 15 m of the resting site was categorized into four main classes: a) “main riverbed”, b) “abstracted water”, c) “standing water” (ponds and wetlands) and d) “tributaries and others” (Fig. A1 in Appendix). Riparian vegetation width was measured at the resting site and the dominant type of vegetation was classified into three categories, namely “natural” (trees, bushes, reed or herbaceous stretches with at least a tree or bush within 25 m along the bank side), “modified” (grass or herbaceous, no trees within 25 m along the bank side) or “artificial” (no vegetation). For the landscape scale, vegetation type was derived from orthophotos with a resolution of 1 m. Classification was made using the tool “Iso Clustering”, an iterative optimization procedure in ArcMap 10, and then verified visually and corrected where necessary. As ground vegetation along water bodies can play a protective role, we incorporated the vegetation period. Onset and end of this period is defined as the daily average temperature >10°C and varies among locations within the study area. Data on vegetation period, daily average temperature and daily snow cover were provided by the GIS office Styria (Austria). Distance to water and to the nearest road were calculated using ArcMap 10. The fine scale anthropogenic disturbance was estimated within 15 m of the resting site on the same bank side by assessing three human types of disturbances (Table 1): 1. D_YEAR: General human presence over the year. 2. D_DAY: Human disturbance throughout the day. 3. D_TYPE: Type of disturbance.

Influence of human disturbance at landscape scale

Human activity and intensity are difficult to measure on a large scale. As humans often restrict their movements to roads (vehicles, bicycles and pedestrians), roads can operate as a proxy for human disturbance. Therefore, we predicted that resting sites should either be further away from the nearest road, or in natural riparian vegetation when close to roads. Availability for each individual was defined as a buffer around the waterbodies within each home range, which was estimated with a 95% fixed kernel (for details see Weinberger *et al.* 2016 and Fig. A2). The width of this buffer was calculated as the 24 m, which equals the mean + 2 SD of the distance of all tracked resting sites to the nearest water body. Where riparian vegetation was missing, we included a buffer of 1 m to ascertain that all types of vegetation were included in the available area but without overrepresentation of the type “artificial”.

For every event an animal was tracked in a resting site, 10 random locations within the available area of each individual were chosen using ArcMap 10. The parameters for model building were selected according to subject-matter knowledge and included habitat type, vegetation type (with “natural” as reference category), vegetation period (categorical variable with “outside vegetation period”=0, and “during vegetation period”=1), temperature, snow cover and distance to the nearest road. Assuming that otters flee into the water only when the source of disturbance is on their bank side, we calculated only the distance to the nearest road on the bank side of the resting site.

Resting site attributes were used for the same date, resulting in the same large-scale weather conditions. This resulted in a matched case-control design, which was then analysed with a conditional logistic regression model (Hosmer & Lemeshow 2004). All predictor covariates used for the models are listed in Table 1 indicated by “A”. Continuous covariates were centered and scaled, resulting in a zero mean and a variance of 1. To obtain population-level parameter estimates, a two-step modelling approach (Fieberg *et al.* 2010) was used by employing automated routines that were provided by the “Ts.estim()” function from the R-package “TwoStepCLogit” (Craiu *et al.* 2011). Animal-specific slopes were included as random effects for each covariate. We used a diagonal between-animal variance-covariance matrix for the random effects, assuming independence among the random slopes. For habitat and vegetation, two categories had to be combined due to low sampling numbers in some animals (Habitat: Main riverbed and abstracted water; Vegetation: modified and artificial). One animal with the lowest variation in the variables had to be removed because its inclusion resulted in the breakdown of the “Ts.estim()” procedure. The analysis was repeated twice, once with the full data set, and once with the data set split into three main seasonal categories (Winter: December-February, Summer: June-August and Intermediate: March-May and September-November) to include the effect of the temperature and assess the importance of the vegetation period.

Influence of human disturbance at local scale

Roads and vehicles may not disturb otters, while human and canine presence may do. This can only be detected at a fine resolution. We assessed the quantity and quality of human disturbance within 15m around the resting sites. For each individual, the same number of resting sites and alternative random locations within the available area was assessed. For all those locations, habitat type, distance to the nearest path (regardless if paved or not), vegetation type and vegetation width were estimated (Table 1, “B”). Additionally, general human presence (D_YEAR), intensity of daily disturbance (D_DAY) and kind of presence (D_TYPE) were estimated within 15 m of the sites. Continuous variables were centered and scaled. A standard logistic regression model was fitted with a binary response variable as indicator for available (0) or used (1) locations. All variables were first included as fixed effects only and the model with the lowest AICc was selected. Finally, all covariates were also included as random effects to allow for animal-specific slopes. Random effects were kept if the AICc was further minimized. A Resource Selection Function (RSF) can then be obtained from

$$RSF = w(x) = exp(\beta_1 x_1 + \ldots + \beta_n x_n),$$

where $x = x_1, \ldots, x_n$ are the predictor covariates included as fixed effects. For any values of the covariates x, w(x) corresponds to the respective proportion between the used and the available frequency (f_u / f_a), and reflects the preference for a habitat with covariates x compared to its availability. Values of $w(x) > 1$ thus represent habitats that were over-proportionally selected by the animal with respect to their availability and w(x) < 1 represents habitats that were avoided.

Selection on the type of resting site structures

Alternatively, the choice of the structure of the resting site itself can vary according to the surroundings. In order to better understand the factors that drive the selection of structures above vs. below ground, a complementary analysis was carried out, where we only used resting sites with known structure type. A logistic regression was applied with the structure as binary response variable (0=below, 1=above ground) and the variables habitat type, vegetation width, vegetation type, distance to nearest path and human disturbances D_YEAR, D_DAY and D_TYPE (Table 1, "C") as explanatory factors.

Results

Between May 2010 to March 2013, nine otters (three males and six females) were radiotracked for more than seven months each (mean duration = 655 days, range 229-1032). Altogether, animals were successfully located on 1814 days (mean=208, 65-399), excluding the 60 occasions (3.2%) when individuals could not be found. Individuals were tracked at 314 distinct resting sites, averaging 33 resting sites per individual (range 13-51, Table A1). Nine resting sites were used by several individuals. Descriptive data could be obtained for 294 of the 314 resting sites. After removing resting sites with missing data, 285 unique resting sites remained. Of those, 271 resting sites (95%) were situated within the riparian vegetation and eight (3%) were either situated in the riparian vegetation disconnected by a hiking path from direct access to the water or were holts in revetments with no vegetation. Only six resting sites (2%) were outside of the riparian vegetation.

Influence of human disturbance at landscape scale

We tested habitat selection of resting sites in relation to human disturbance (using distance to roads as proxy) at the landscape scale. With data from all seasons combined, there was a very strong evidence for the avoidance for tributaries ($p < 0.001$, Table 2). When accounting for seasonal effects, the clear avoidance of tributaries was consistent, except in summer. We did not find evidence for the influence of the distance to roads ($p=0.14$ in the model for all seasons combined). However, resting sites tended to be closer to roads in summer when vegetation is highest.

Influence of human disturbance at local scale

As tributaries were negatively selected at the landscape scale, availability was subset to the habitats main riverbed, standing waters and abstracted water (n = 284 resting sites). The model with lowest AICc included the variables vegetation width (VWIDTH), distance to the nearest path (DistP), habitat type, the intensity of the disturbance (D_TYPE) and the interaction between D_DAY and vegetation width, and an animal-specific random slope for the distance to the nearest path (Table 3, for the three models with lowest AICc see Table A2). Human presence throughout the day (D_DAY) appeared to influence the choice of resting site locations concerning the vegetation width (Fig. 3). Here, the most extreme values of human presence had the clearest impact: Animals chose resting sites with small riparian vegetation width when there was no daily human disturbance (Fig. 3a), where animals preferred to rest in areas with vegetation widths up to 10m. However, when there was a high frequency of daily human disturbance, the selection was reversed, i.e. otters then apparently preferred areas with larger vegetation width, although the uncertainty in the RSF was large (Fig. 3d). Even in the presence of intermediate disturbances, the otters appear to be attracted by generally larger vegetation belts than when undisturbed (estimate = 0.73, $p=0.002$ and estimate = 0.67, $p=0.041$, respectively), but the confidence bands span a large area (Fig. 3b and c) without indication of a clear preference. Compared to random locations, animals preferred areas with natural vegetation type, which is visible by the clearly negative selection of modified vegetation (estimate = -2.29, $p<0.001$) or no vegetation (estimate = -1.6, $p=0.005$). There is some evidence that resting sites were further away from roads (estimate = 0.39, $p = 0.049$), and that the intensity of human disturbance has an impact ($p = 0.042$). We have only little evidence that the suspected effect of dogs as increased perceived risk is important (estimate = -0.88, $p=0.116$).

Selection of resting site structures

For 262 (of 294) resting sites, the respective structure could be assessed. 102 resting sites (40%) were situated above ground and 160 resting sites were below ground.

The best model to explain the use of the different resting site structures included vegetation period, distance to nearest path, temperature and the interaction of riparian vegetation width with the intensity of daily disturbance (Table 4; for the best three models with lowest AICc, see Table A3). Outside of the vegetation period, animals were more likely to sleep below ground than above (estimate = -0.858, $p < 0.001$). Distance to roads was larger for resting sites above ground than below (estimate = 0.574, $p < 0.001$). There was clear evidence that human disturbance in combination with vegetation width appeared to shape the selection of resting site structures in a relevant way. Animals slept more likely above ground when there was no disturbance. At sites with low to moderate human disturbance (once a day and every few hours, resp.), resting sites were more likely to be situated below ground and with increasing vegetation belt width (estimates = 0.310 and -3.081, $p = 0.024$ and < 0.001). However, where human disturbance was permanent, preference was reversed with sites preferred above ground but large vegetation width (estimate = 1.369, $p = 0.071$).

Discussion

Our study highlights the importance of riparian vegetation cover for a nocturnal carnivore in human dominated landscapes. Its naturalness and width is crucial because it also functions as a protection against human disturbance. Indeed, our results show that humans shape the resting site selection of otters. At low levels of daily human presence, riparian vegetation width can be marginal for resting otters. However, once humans move around a resting site at high frequencies throughout the day, the importance of a wide riparian vegetation width increases, indicating that resting otters do perceive humans as risk factor. At mediate levels of daily disturbance, resting sites are distributed over the whole range of vegetation width. This large variance could be due to a) an artefact of the determination of the intensity of daily disturbance or b) a compensatory effect of the structure of the resting site.

The assessment of “no disturbance” at any time during the day and “permanent disturbance” was relatively easy (e.g. no visible path, factory with high turnover of workers throughout the day). However, the assignment to “low” or “mediate” intensity of daily disturbance was estimated on the perception of the observer and may be too arbitrarily.

For otters, the effect of human presence on general habitat selection has yielded controversial results, with studies indicating a tolerance for human presence (Green, Green & Jefferies 1984; Durbin 1998; Kruuk 2006; Bedford 2009) and others an avoidance (Barbosa *et al.* 2001; Prenda, Lopez-Nieves & Bravo 2001; Baltrulnaite *et al.* 2009). However, many studies used different variables to measure human disturbance, e.g. roads (e.g. Durbin 1998), houses (Baltrulnaite *et al.* 2009; Juhász *et al.* 2013) or human densities/km^2 and road densities/km^2 (Barbosa *et al.* 2001). In our study, the distance to roads played a significant role at the level of the resting site and at the level of the structure but not at the landscape scale. This is could be attributed to the lower categorical resolution of the spatial data for the latter: Geographical information was available for paved roads intended for motorized traffic, but not for pedestrian paths and private roads. At the level of the resting site, the nearest path was assessed by the observer, regardless its function. Our study shows the strength of the multi-scale approach but also its difficulty to apply management on a large scale if data is not available for the finest scale.

The selection of resting site structure also indicates a perceived threat by humans. The influence of vegetation cover is much stronger than temperature. Thus the selection of the resting site structure seems to be driven by the lack of vegetation and therefore by the lack of protection from predators. This is different to other studies which stressed the importance of thermal cover characteristics in medium sized mammals (Weber 1989; Brainerd *et al.* 1995; Baghli & Verhagen 2005). However, selection of resting site structure depending on weather conditions may have gone unnoticed here as otters may use holts also during peaks of hot weather. Dense fur can implicate overheating problems, because otters dissipates heat only through the small body surface of its feet, therefore restricting heat loss (Kuhn & Meyer 2009).

Our results are in accordance with studies on resting site selection of other carnivores where the impact of small scale human disturbance was dependent on vegetation (Sunde, Stener & Kvam 1998; Ordiz *et al.* 2011). Nocturnal animals require protected resting sites in a human dominated landscape. In areas devoid of natural vegetation cover like hedges and forests, the riparian landscape provides the only remaining cover structure for wildlife. Exactly this vegetation belt is disappearing in many areas due to intensification in agriculture, flood management and urbanization. Our finding contributes to other studies on different animal species where the riparian vegetation is of major importance (Naiman, Decamps & Pollock 1993; Semlitsch & Bodie 2003; Matos *et al.* 2009; Bennett, Nimmo & Radford 2014), stressing the need for conservation actions for the riparian vegetation and thus facilitating the recovery of an endangered semi-aquatic carnivore.

Conclusions

An intact riparian vegetation belt is a crucial element for wildlife. Especially in an anthropogenic altered landscape, animals need protection against human disturbance. With our work, we show that otters require a natural riparian vegetation. The width of this vegetation belt becomes more important at locations with intensive human presence. Restricted and fragmented natural landscapes and limited financial funding are main issues in conservation management. Therefore, knowledge of the quality of habitat patches is crucial to preserve species and communities. Our result on the distinctive requirements of the resting sites of otters within a human dominated landscape can help formulate guidelines for revitalisation projects. A potential management policy could be to a) establish or conserve patches with riparian vegetation where human access is restricted or b) create patches with riparian vegetation as buffers where humans are present.

Acknowledgements

This study was promoted by the foundation Pro Lutra, Switzerland and funded by Zuercher Tierschutz, Ernst Goehner Stiftung, Stotzer-Kaestli-Stiftung, Bernd Thies-Stiftung, Autax-

Stiftung, Stiftung Temperatio, Conseil International de la Chasse CIC, Sektion Schweiz, Theo-Wucher Stiftung, Charlotte und Nelly Dornacher Stiftung, Peter Weinberger and an anonymous sponsor. Environmental data was provided by GIS Steiermark (Divison 7). Authorization for capture and treatment of otters was given by the government of Styria, Austria (Division 10a and 13c). We are very indebted to Susana Freire, Barbara Schnueriger, André Weller, Susanne Pusch, Gaspar Camlik, Vaslik Beran, Lucas Polednik, Ales Toman Annette Stephani, Iris Hanetseder and Lisa Spuehler for their fieldword. We thank Addy and Lena de Jongh and Tjibbe Jong for capturing and Ronald Schmidt for support in GIS.

References

Baghli, A. & Verhagen, R. (2005) Activity patterns and use of resting sites by polecats in an endangered population. *Mammalia*, **69**, 211–222.

Baltrulnaite, L., Balciauskas, L., Matulaitis, R., Stirke, V., Baltrūnaitė, L., Balčiauskas, L. & Stirkė, V. (2009) Otter distribution in Lithuania in 2008 and changes in the last decade. *Estonian Journal of Ecology*, **58**, 94.

Barbosa, A.M., Real, R., Marquez, A.L. & Rendon, M.A. (2001) Spatial, environmental and human influences on the distribution of otter (Lutra lutra) in the Spanish provinces. *Diversity and Distributions*, **7**, 137–144.

Bedford, S.J. (2009) The effects of riparian habitat quality and biological water quality on the European Otter (Lutra lutra) in Devon. *Bioscience Horizons*, **2**, 125–133.

Beja, P.R. (1996) Temporal and spatial patterns of rest-• site use by four female otters Lutra lutra along the south-west coast of Portugal. *Journal of Zoology*, **239**, 741–753.

Bennett, A.F., Nimmo, D.G. & Radford, J.Q. (2014) Riparian vegetation has disproportionate benefits for landscape-scale conservation of woodland birds in highly modified environments. *Journal of Applied Ecology*, **51**, 514–523.

Blanc, R., Guillemain, M., Mouronval, J.B., Desmonts, D. & Fritz, H. (2006) Effects of non-consumptive leisure disturbance to wildlife. *Revue d'Ecologie (La Terre et la Vie)*, **61**, 117–133.

Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M. & Holekamp, K.E. (2003) Altered behaviour in spotted hyenas associated with increased human activity. *Animal Conservation*, **6**, 207–219.

Brainerd, S.M., Helldin, J.O., Lindstrom, E.R., Rolstad, E., Rolstad, J. & Storch, I. (1995) Pine marten (Martes martes) selection of resting and denning sites in Scandinavian managed forests. *Annales Zoologici Fennici*, **32**, 151–157.

Brown, J.S., Laundre, J.W. & Gurung, M. (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, **80**, 385–399.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J. a. & Boyce, M.S. (2012) Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLoS ONE*, **7**.

Coetzee, B.W.T. & Chown, S.L. (2015) A meta-analysis of human disturbance impacts on Antarctic wildlife. *Biological Reviews*, doi: 10.1111/brv.12184

Comiti, F. (2012) How natural are Alpine mountain rivers? Evidence from the Italian Alps. *Earth Surface Processes and Landforms*, **37**, 693–707.

Craiu, R. V., Duchesne, T., Fortin, D. & Baillargeon, S. (2011) Conditional Logistic Regression With Longitudinal Follow-up and Individual-Level Random Coefficients: A Stable and Efficient Two-Step Estimation Method. *Journal of Computational and Graphical Statistics*, **20**, 767–784.

Durbin, L.S. (1998) Habitat selection by five otters Lutra lutra in rivers of northern Scotland. *Journal of Zoology London*, **245**, 85–92.

ESRI. (2011) ArcGIS Desktop: Release 10.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M.S. & Frair, J.L. (2010) Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2233–44.

Foster-Turley, P., Macdonald, S.M. & Mason, C.F. (1990) *Otters: An Action Plan for Their Conservation*. IUCN Otter Specialist Group.

Frid, A. & Dill, L. (2002) Human-caused disturbance as a form of predation risk. *Conservation Ecology*, **6**.

Green, J., Green, R. & Jefferies, D. (1984) A radio-tracking survey of otters Lutra lutra on a Perthshire river system. *Lutra*, **27**, 86–145.

Hosmer, D.W. & Lemeshow, S. (2004) *Applied Logistic Regression*. Wiley, New York.

Janssens, X., Defourny, P., De Kermabon, J. & Baret, P. (2006) The recovery of the otter in the Cevennes (France): a GIS-based model. *Hystrix-the Italian Journal of Mammalogy*, **17**, 5–14.

Juhász, K., Lukács, B.A., Perpék, M., Nagy, S.A. & Végvári, Z. (2013) Effects of extensive fishpond management and human disturbance factors on Eurasian otter (Lutra lutra L. 1758) populations in Eastern Europe. *North-Western Journal of Zoology*, **9**, 227–238.

Kienast, F., Degenhardt, B., Weilenmann, B., Wäger, Y. & Buchecker, M. (2012) Landscape and Urban Planning GIS-assisted mapping of landscape suitability for nearby recreation, **105**, 385–399.

Kranz, A. & Poledník, L. (2012) *Fischotter Verbreitung und Erhaltungszustand 2011 im Bundesland Steiermark.* Endbericht. Graz

Kranz, A. & Poledník, L. (2015) *Fischotter in Kärnten: Verbreitung & Bestand 2014*. Graz

Kruuk, H. (1995) *Wild Otters: Predation and Populations*. Oxford University Press Inc., Oxford UK.

Kruuk, H. (2006) *Otters: Ecology, Behaviour and Conservation*. Oxford University Press Inc., New York.

Kuhn, R.A. & Meyer, W. (2009) Infrared thermography of the body surface in the Eurasian otter Lutra lutra and the giant otter Pteronura brasiliensis. *Aquatic Biology*, **6**, 143–152.

Laundré, J., Hernández, L. & Ripple, W. (2010) The landscape of fear: ecological implications of being afraid. *Open Ecology Journal*, **2**, 1–7.

Llaneza, L., García, E.J., Palacios, V., Sazatornil, V. & López-Bao, J.V. (2016) Resting in risky environments: the importance of cover for wolves to cope with exposure risk in human-dominated landscapes. *Biodiversity and Conservation*.

Manning, A.D., Gibbons, P., Fischer, J., Oliver, D.L. & Lindenmayer, D.B. (2013) Hollow futures? Tree decline, lag effects and hollow-dependent species. *Animal Conservation*, **16**, 395–403.

Matos, H., Santos, M., Palomares, F. & Santos-Reis, M. (2009) Does riparian habitat condition influence mammalian carnivore abundance in Mediterranean ecosystems? *Biodiversity and Conservation*, **18**, 373–386.

Mccormick, A., Fisher, K. & Brierley, G. (2015) Quantitative assessment of the relationships among ecological , morphological and aesthetic values in a river rehabilitation initiative. *Journal of Environmental Management*, **153**, 60–67.

Murphy, G.E.P. & Romanuk, T.N. (2014) A meta-analysis of declines in local species richness from human disturbances. *Ecology and*, **4**, 91–103.

Mysterud, A. & Østbye, E. (1999) Cover as habitat Element for Temperate Ungulates : Effects on Habitat Selection and Demography. *Wildlife Society Bulletin*, **27**, 385–394.

Naiman, R., Decamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. *Ecological applications*, **3**, 209–212.

Ó Néill, L., de Jongh, A., Ozoliņš, J., Jong, T. De & Rochford, J. (2007) Minimizing Leg-Hold Trapping Trauma for Otters With Mobile Phone Technology. *Journal of Wildlife Management*, **71**, 2776–2780.

Ordiz, A., Stoen, O.-G., Delibs, M. & Swenson, J.E. (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**, 59–67.

Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015) Landscapes of Coexistence for terrestrial carnivores : the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, 1–11.

Prenda, J., Lopez-Nieves, P. & Bravo, R. (2001) Conservation of otter (Lutra lutra) in a Mediterranean area: the importance of habitat quality and temporal variation in water availability. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **11**, 343 – 355.

Prigioni, C., Balestrieri, A. & Remonti, L. (2007) Decline and recovery in otter Lutra lutra populations in Italy. *Mammal Review*, **37**, 71–79.

Reichman, O.J. & Smith, S.C. (1990) Burrows and burrowing behavior by mammals. *Current Mammalogy* (ed H.H. Genoways). Plenum Press, London.

Rey Benayas, J.M. & Bullock, J.M. (2015) Vegetation Restoration and Other Actions to Enhance Wildlife in European Agricultural Landscapes. *Rewilding European Landscapes*, 1st ed (eds H.M. Pereira), & L.M. Navarro), pp. 127–142. Springer Berlin Heidelberg.

Semeniuk, C.A.D. & Dill, L.M. (2005) Cost/benefit analysis of group and solitary resting in the cowtail stingray, Pastinachus sephen. *Behavioral Ecology*, **16**, 417–426.

Semlitsch, R.D. & Bodie, J.R. (2003) Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles. *Conservation Biology*, **17**, 1219–1228.

Sunde, P., Stener, S.O. & Kvam, T. (1998) Tolerance to humans of resting lynxes Lynx lynx in a hunted population. *Wildlife Biology*, **4**, 177 – 183.

Weber, D. (1989) The ecological significance of resting sites and the seasonal haibtat change in polecats (Mustela putorius). *Journal of Zoology London*, **217**, 629–638.

Weinberger, I.C., Muff, S., de Jongh, A., Kranz, A. & Bontadina, F. (2016) Flexible habitat selection paves the way for a recovery of otter populations in the European Alps. *Biological Conservation*, **199**, 88–95.

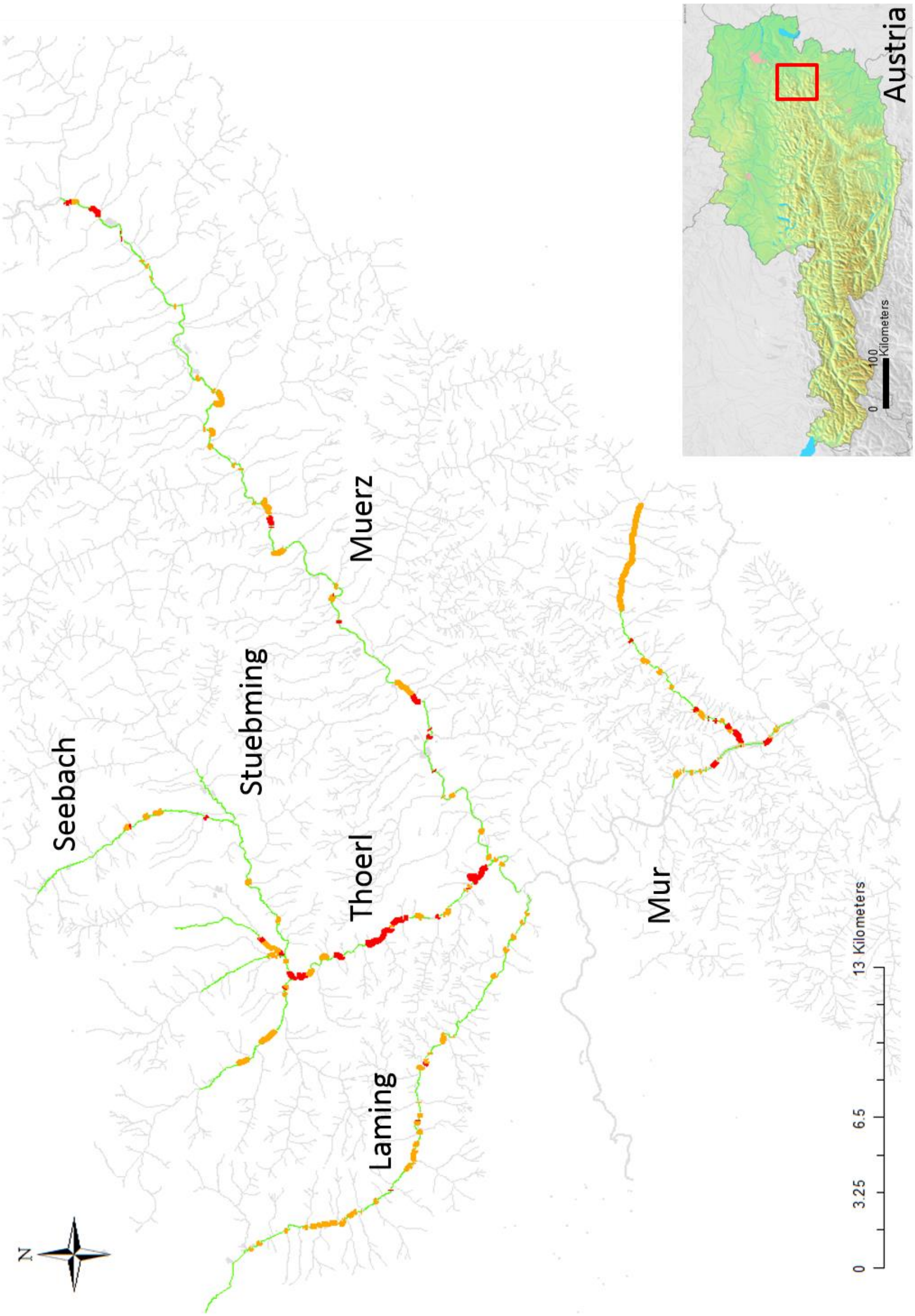


Figure 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters showing the running and standing water bodies. Vegetation type of all main riverbeds within any home ranges was assessed: green = natural vegetation, orange = modified and red = artificial (no vegetation).

Table 1. Day resting sites: Overview of the structure, habitat and disturbance variables used in the analyses. Environmental variables used for the different analyses are indicated with A=large scale human disturbance, B=fine scale human disturbance and C=structures

Variables	Code	Description	Measurement	Analyses
Habitat type		Four categories within the water course: a) Main riverbed b) Abstracted water (Water derived from the dam reservoir to the hydroelectric power station (head water) and from there (tail water) back to the main riverbed c) Standing water such as ponds d) Tributaries (small streams flowing in the main river within the home range)	Categorical	A, B
Vegetation period	VEGPER	Onset and end of the vegetation period when mean daily temperature is > 10°C. Resolution at 50m for the study area	Categorial (0 = outside, 1 = during vegetion period)	A, B
Temperature	T	Daily mean temperature from nearest weather station (five stations over the whole area)	Continous	A,
Snow cover	SNOW	Daily snow cover, data from the nearest weather station (five stations over the area)	Continous	A, C
Distance to roads	DistR	Paved roads	Meters	A
Distance to path	DistP	Path or roadlike structure (from hiking path to highway)	Meters	B, C
Vegetation type	VTYPE	Naturalness of the type of riparian vegetation: natural (forest, reed, herbacous stretches with at least 1 tree/bush within 25m), modified (herbacous, meadow, grass) and no vegetation)	Ordinal (1-3, with 1=natural, 2=foreign and 3 = no vegetation)	B
Vegetation width	VWIDTH	Width of natural or semi-natural vegetation measured from waterside	Continous	B, C
Intensity of disturbance over the year	D_YEAR	Human presence occurring over the year.	Ordinal (1-3, with 1 = never, 2=occasionally and 3=daily)	B, C
Intensity of daily Disturbance	D_DAY	Human disturbance throughout the day	Ordinal (1-4, with 1=none, 2 = once a day, 3=every few hours, 4=permanent or min. 1 every 2 hours)	
Type of daily disturbance	D_TYPE	Type and intensity of disturbance	Ordinal (1-4, with 1=none, 2=working, 3=spare time and 4 = spare time with dogs)	

Table 2. Results from the two-step conditional analysis of habitat selection of resting sites at landscape scale (N=8 individuals, one animal had to be removed from the analyses because of statistical reasons, details see methods).

All seasons combined

Variables	**Estimate**	**Std. Error**	**p-value (Wald)**
Tributaries	-2.765	0.880	0.001
Standing water	0.364	1.024	0.361
Distance to roads	0.125	0.117	0.143
Modified & no vegetation	-0.619	0.355	0.041

Winter

Variables	Beta	SD	p-value (Wald)
Tributaries	-5.086	0.773	< 0.001
Standing water	-1.306	1.143	0.127
Distance to roads	0.145	0.117	0.108
Modified & no vegetation	-0.399	0.692	0.282

Intermediate season

Variables	Beta	SD	p-value (Wald)
Tributaries	-3.125	0.876	< 0.001
Standing water	0.169	1.050	0.436
Distance to roads	0.126	0.139	0.182
Modified & no vegetation	-0.441	0.353	0.106

Summer

Variables	Beta	SD	p-value (Wald)
Tributaries	-1.896	1.484	0.101
Standing water	0.705	1.004	0.241
Distance to roads	-0.045	0.233	0.423
Modified & no vegetation	-0.219	0.281	0.217

Table 3. Summary of the best model selected for selection of resting sites at the fine scale. Variables in italics show the overall value (including the reference category) of the term in the model (chi-square value).

Variables	**Estimate**	**SE**	**z**	**p**
VWIDTH	-0.740	0.147	-5.022	< 0.0001
VTYPE				<0.0001
Modified (p< 0.001)	-2.289	0.474	-4.831	
No vegetation (p=0.005)	-1.598	0.566	-2.825	
Interaction VWIDTH:D_DAY				0.0004
VWIDTH:once a day (p=0.002)	0.729	0.237	3.075	
VWIDTH:every few hours (p=0.041)	0.660	0.322	2.048	
VWIDTH:permanent (p=0.002)	2.142	0.686	3.125	
DistP	0.389	0.198	1.965	0.049
HABITAT TYPE				0.048
SIDE (p=0.085)	1.477	0.856	1.724	
STILL (p=0.537)	0.249	0.403	0.618	
D_DAY				0.012
once a day (p=0.398)	0.378	0.448	0.844	
every few hours (p=0.356)	-0.481	0.521	-0.924	
permanent(p=0.329)	-0.603	0.618	-0.975	
D_TYPE				0.042
working (p=0.743)	-0.152	0.463	-0.327	
spare time (p=0.098)	-0.909	0.549	-1.656	
dog (p=0.116)	-0.879	0.560	-1.571	

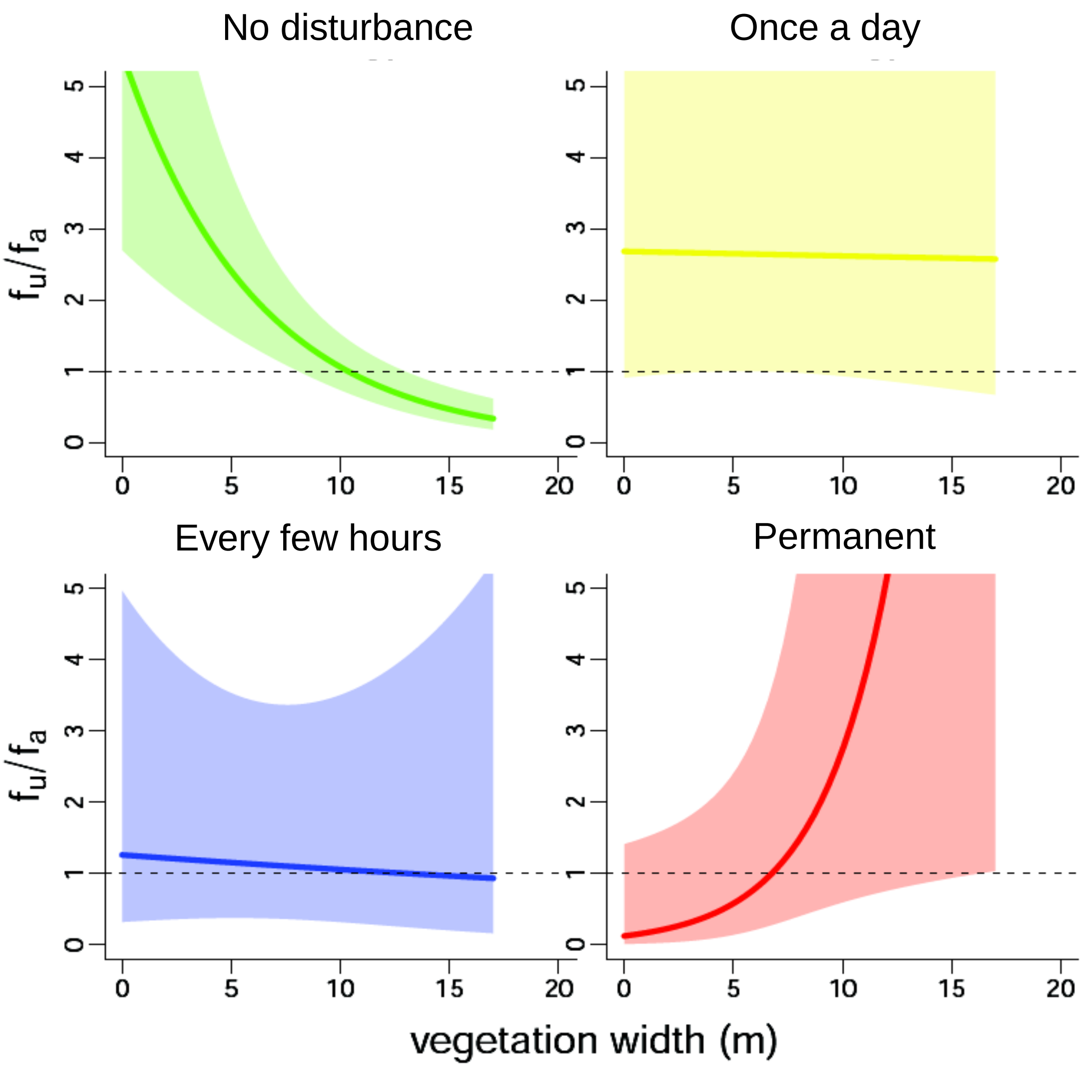


Figure 3. Vegetation width at resting site locations depending on the intensity of daily human disturbance in natural riparian vegetation: a) to d) increasing daily disturbance with a) no disturbance, b) once a day, c) every few hours and d) permanent human presence. The Plot shows the regression line and the 95% confidence bands.

Table 5. Summary of the best model, with resting site structure as the response variable (0= below ground, 1=above ground resting sites). Variables in italics show the overall value (including the reference category) of the term in the model (chi-square value).

Variables	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
VWIDTH	0.366	0.118	3.104	0.001
VEGPER (<0.001)				
Outside vegetation period	-0.858	0.200	-4.297	< 0.001
Distance to roads	0.574	0.071	8.132	< 0.001
D_DAY (<0.001)				
Disturbance once a day	0.002	0.144	0.014	0.989
Disturbance every few hours	-2.510	0.737	-3.406	< 0.001
Permanent disturbance	0.211	0.623	0.338	0.735
Temperature	-0.194	0.103	-1.886	0.059
VWIDTH (< 0.001)				
VWIDTH: Disturbance once a day	-0.310	0.137	-2.260	0.024
VWIDTH: Disturbance every few hours	-3.081	0.782	-3.940	< 0.001
VWIDTH: permanent disturbance	1.369	0.757	1.808	0.071

Appendix

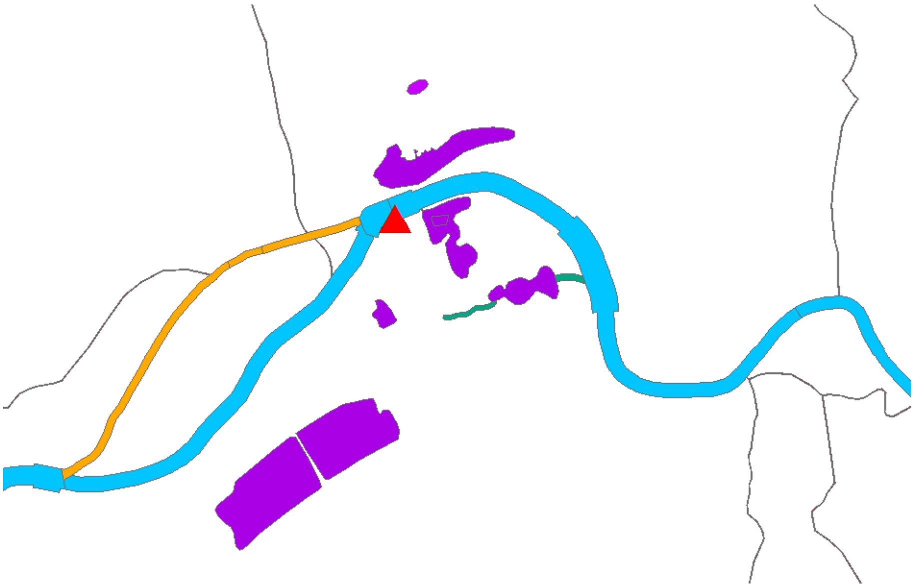


Figure A1. Classification of the main water bodies. Blue= main riverbed, yellow = abstracted water, grey= tributaries and lilac=standing water. The red triangle signifies the weir, where the abstracted water is deviated from the main riverbed.

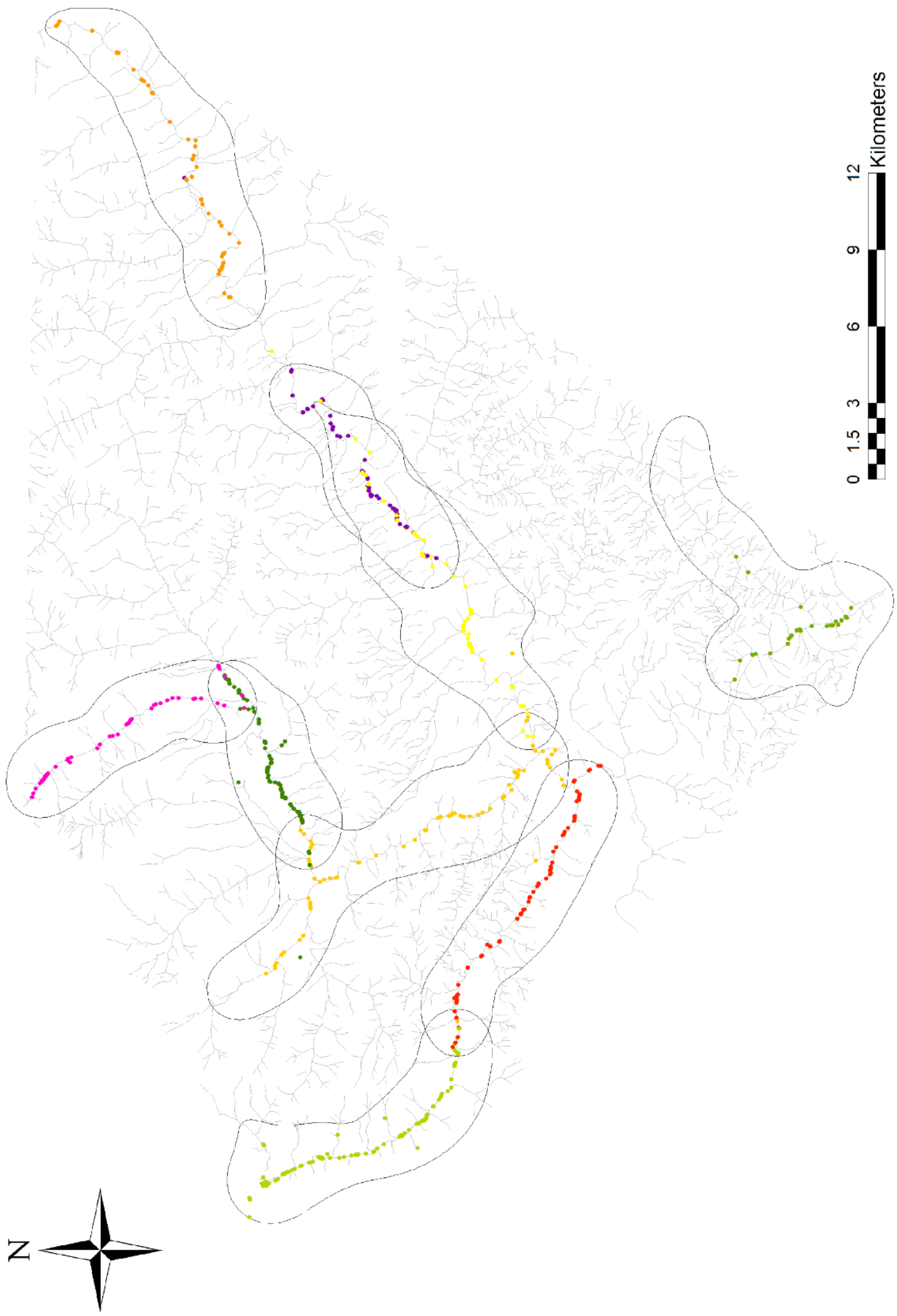


Figure A2. Distribution of resting sites for all radiotracked otters (colours indicate individuals) within their respective home range using fixed kernel estimator at 95%, shown as black lines. Grey lines indicate the watercourses within the study area.

Table A1. Information on number of tracked animals and resting site locations over the whole tracking period. For 20 resting sites, not enough data could be collected (Table 2), resulting in 285 individual resting sites. Nine resting sites were used by two individuals and were treated independently for each individual for further analyses, increasing the sample size to 294 resting sites.

Animal	Sex	Age at Capture	Start Tracking	End Tracking	Individual day locations	Mean daytime locations/week	Total Resting Sites (data deficient/shared)	RS analysed
Alena	F	Sub-adult	08/05/2010	05/03/2013	399	3.08	54 (3/0)	51
Baukje	F	Adult	07/11/2010	05/03/2013	279	2.58	36 (2/1)	34
Cleo	F	Sub-adult	10/11/2010	15/06/2012	195	2.58	44 (3/0)	41
Dan	M	Adult	10/11/2010	07/03/2013	233	2.27	44 (2/1)	42
Fee	F	Sub-adult	03/05/2011	21/03/2013	189	2.20	26 (2/0)	24
Gessa	F	Adult	03/05/2011	18/03/2013	181	2.27	33 (2/2)	31
Hans	M	Adult	07/05/2011	09/03/2013	185	2.29	36 (1/5)	35
Ivo	M	Adult	14/04/2012	21/02/2013	88	2.33	27 (4/0)	23
Johanna	F	Adult	14/04/2012	29/11/2012	65	2.14	14 (1/0)	13
Total					**1814**	**2.41**	**314 (20/9)**	**294**

Table A2. Best models for fine scale resting site selection according to the corrected Akaike's Information Criterion (AICc). K is the number of estimated parameters for each model. The ranking of the models is based on differences in AICc (Delta AICc).

Models	AICc (K)	Delta AICc (wi)
HABITAT + VWIDTH + VTYPE + D_DAY + D_TYPE + DistR + D_DAY:VWIDTH	698.40 (17)	0 (0.59)
VWIDTH + VTYPE + D_DAY + D_TYPE + DistR + D_DAY:VWIDTH	700.22 (15)	1.83 (0.24)
HABITAT + VWIDTH+ VTYPE + D_DAY + D_TYPE + DistR + D_DAY:VWIDTH+ D_TYPE:VWIDTH	701.05 (20)	2.6 (0.15)

Table A3. Best models for fine scale resting site selection according to the corrected Akaike's Information Criterion (AICc). K is the number of estimated parameters for each model. The ranking of the models is based on differences in AICc (Delta AICc).

Models	**AIC c (K)**	**AICc (wi)**
VWIDTH + D_DAY + VEGPER + DistR + T + VWIDTH : D_DAY	1908.101 (12)	0.00 (0.50)
VWIDTH + D_DAY + D_YEAR + VEGPER + DistR + T + VWIDTH : D_DAY	1908.112 (14)	0.012 (0.49)
VWIDTH + D_TYPE + VEGPER + DistR + T + VWIDTH : D_TYPE + VWIDTH : VEGPER	1919.186 (13)	11.09 (0.01)

Chapter 4

Multi-scale habitat suitability modelling for otters in the Alpine Arc

Irene C. Weinberger, Stefanie Muff, Andreas Kranz & Fabio Bontadina

From here to there – Modelling habitat suitability where the species is still largely absent

Abstract

Predictive distribution modelling is important to estimate the potential of a spatial expansion of a population. It is also used to target conservation measures for recovering species. Predictive habitat modelling is especially relevant for carnivores because of their importance for maintaining ecosystem functions.
The Eurasian otter is a semi-aquatic top predator. Its populations have declined drastically within the 20th century, with extinctions in several countries and landscapes of Western Europe, including the Alpine Arc. Habitat loss, pesticides and persecution are considered to be the main causes for the decline. Recently, populations have started to re-expand, e.g. in Austria and France. Switzerland, lying at the core of the Alps, plays thus a crucial role in reconnecting the populations of the West (France) and East (Austria). Therefore, we aimed to assess the habitat suitability to predict and facilitate the recovery of the species in Switzerland.
HSMs are scale-sensitive because the effect of environmental variables can vary depending on the spatial scale (Collingham *et al.* 2000). Multi-scale approaches may compensate this deficit as it is crucial to detect the most informative scale of in order to understand habitat selection (Wiens 1989). However, the multi-scale approach has only recently received attention (du Toit 2010).
We developed two habitat suitability maps (HSMs) at two different resolutions. For the coarse HSM, we used snow tracking data of otters at a resolution of 10 km^2 in the Austrian Alps. Data on resting site selection of nine radiotracked otters in parts of the Austrian Alps contributed to the fine scale habitat selection. We then applied both HSMs to Switzerland. Both HSMs yielded suitable habitat in Switzerland and predicted a connectivity within the country. Habitat suitability differed in regions depending on scale. Human related variables had negative effects at the large scale on otter occurrence, which resulted in a low habitat suitability in the north of Switzerland, where over $^2/_3$ of the Swiss human population lives. At the fine scale, otter presence was predicted by naturalness of the watercourse and the distance to roads. At this scale, otters are more tolerant of humans, thus reversing some of the results by the coarse HSM.
Our models offer a tool to identify conservation requirements especially at the fine scale level, which can guide regional or national conservation schemes.

Introduction

Conservation efforts such as adequate protection, habitat preservation or restoration and reduction in toxic components in the environment can lead to a positive trend in endangered species (e.g. Hutson et al. 2001; McAlpine et al. 2006; Robbins et al. 2011). In recent decades, species have even returned to areas, where they have long been absent e.g. species of whales (Clapham, Young & Brownell 1999), birds (Le Corre *et al.* 2015) and carnivores (Chapron *et al.* 2014).

Important components for the re-expansion of an endangered population are suitable habitat at the periphery of the current distribution and the continuous connectivity of the landscape matrix outside the periphery. Habitat suitability models (HSM), also called species distribution models (SDM), have become important conservation tools to predict suitable habitat and its connectivity within the landscape matrix and to identify barriers (Araújo & Williams 2000; Rushton, Merod & Kerby 2004). The conservation goal is usually focused on specific levels like global, national, regional or local levels (Cabeza *et al.* 2010). Scale, however, is an important factor in habitat suitability modelling. Environmental parameters are scale-sensitive (Collingham *et al.* 2000) and can thus yield different results depending on the resolution. The scale, at which an HSM is built, influences the scale at which the specific conservation actions can be addressed: It has been shown that conservation efforts are most efficient when applied at several scales (Poiani *et al.* 2000), but the multi-scale approach of HSM has only recently received increasing attention (du Toit 2010).

Predictive distribution modelling is relevant for identifying conservation requirements and potential distribution of carnivores because of their large activity ranges and their potential of conflict with humans (Woodroffe 2000). After massive population declines in the last two centuries, the importance of the restoration of carnivore populations has been widely recognized for maintaining ecosystem functions (Ripple *et al.* 2014). Where policies towards carnivores have shifted away from active persecution, some carnivore species recolonize parts of their historical range, e.g. wolves *Canis lupus*, brown bear *Ursus arctos*, and European lynx *Lynx lynx* (Musiani & Paquet 2004; Chapron *et al.* 2014).

One of the important issues for a successful recovery is thus whether the still abandoned landscapes offer suitable and abundant habitat. Predictive habitat suitability can be an instrument to detect potential areas for recovery in mobile species or to define areas to implement conservation measures.

One of the re-expanding carnivore species is the Eurasian otter *Lutra lutra* in Western Europe. The otter is a semi-aquatic apex predator, which suffered strong declines in the 20th century in Western Europe (Foster-Turley, Macdonald & Mason 1990). Reasons for the decline were attributed to persecution, environmental pollutants and habitat degradation (Foster-Turley, Macdonald & Mason 1990; Kruuk 2006). The otter is listed as “Near

Threatened" on the IUCN red list of Europe (Temple & Terry 2007) and further protected under the EC Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC). In recent decades, a slow recovery of the populations was observed (Cortés *et al.* 1998; Kranz & Toman 2000; Prigioni *et al.* 2008). This has led to the development of several habitat suitability models for otters: e.g. Europe (Robitaille & Laurence 2002; Cianfrani *et al.* 2011), Czech Republic (Marcelli *et al.* 2012), France (Janssens *et al.* 2006; Van Looy *et al.* 2013), Germany (Klenke 1998), Hungary (Kemenes & Demeter 1995), Italy (Ottino, Prigioni & Taglianti 1995; Prigioni 1995; Remonti *et al.* 2008; Loy *et al.* 2009; Marcelli & Fusillo 2009; Ottaviani *et al.* 2009; Cianfrani *et al.* 2010; Carranza *et al.* 2012; Carone *et al.* 2014) and Switzerland (Cianfrani *et al.* 2013).

Otters in European freshwater ecosystems are nocturnal and elusive, which makes them extremely difficult to study. Their distribution is therefore often assessed using the standard otter survey methodology, which requires that searches for signs such as faeces (spraints) are conducted along a 600m transect of river bank or lake shore (Mason & MacDonald 1986). This widely used monitoring scheme is designed to assess the distribution of otters at broad scales (e.g. 10km^2), because the probability of detection at a single transect is <30% for a single visit (Parry *et al.* 2013). Virtually all HSM for otters are relying on indirect observations such as spraints or expert-based knowledge and are developed at a single scale.

In the Alpine Arc, the otter was nearly gone with only few individuals remaining at the edge of the Alps (Foster-Turley, Macdonald & Mason 1990). In the last few decades, the otter populations have expanded again (Kranz 2000; Kranz *et al.* 2013; Kranz & Poledník 2015) and the first scouting individuals have been even sighted recently in Switzerland (see www.prolutra.ch), where the species got extinct in 1989 (Weber 1990). As Switzerland is at the core of the Alps and is central to the reconnection of the expanding populations in the South (Italy), West (France) and East (Austria), it is crucial to understand the species' habitat requirements and availability in the Alpine Arc.

Our objective for this study was to provide a spatial description of habitat quality for otters in the Alps to locate highly suitable areas and to facilitate information on habitat requirements for conservation management. Additionally to the traditional coarse scale used for otter habitat suitability models, we aimed to identify fine scale habitat suitability at the behavioural level. We thus developed habitat suitability models at two spatial scales with data derived from different sampling strategies. For the coarse scale habitat suitability model, data came from surveys conducted at a 10km^2 scale (Kranz & Poledník 2010; Kranz *et al.* 2013). A radiotracking study of wild otters was conducted in Styria, Austria, to provide the data for the fine scale habitat suitability model. Although in general otter presence is defined by fish abundance (Clavero, Blanco-Garrido & Prenda 2005), at an even finer scale otter presence may be limited by suitable habitat for resting sites (see Chapter 3). Therefore, we concentrated our efforts for the fine scale habitat suitability on resting site selection.

Method

Study area

For the large scale modelling, the area of Styria, Austria, at the Central Eastern Alps of the European Alpine Arc and Switzerland was used. Styria has an area of 16'400 km^2, with approx. 74 inhabitants per km^2. 60% of the land is covered with forest. Winters are cold with an average temperature of -2.5°C and warm summers with mean temperature of 17.9°C at 500 masl (Wakonigg *et al.* 2010). There are over 6600 watercourses with a total length of approx. 17'200 km. The landscape varies from rolling hills and high human density in the southern part of Styria to an alpine character in the northern part, where mountain peaks reach up to 2990 masl and human density is low. Projection of the data was done to Switzerland, which is situated in the core of the Alpine Arc. It covers 41'290 km^2 and has an average human density of 188/km^2.

For the fine scale study, radiotracking was conducted from May 2010 to March 2013 in the eastern Central Alps in Styria, Austria in the area of Bruck an der Mur (N47°24'36", E15°16'7"; Fig. 1). The area covers 1760 km^2, with about 3090 km length of watercourses. All watercourses here belong to the catchment basin of the river Mur, which has a mean annual discharge of approx. 110 m^3/s. The main valley in the study area is the Muerz valley named after the river Muerz with a mean annual discharge of 20 m^3/s. The rivers and streams is mainly inhabited by brown trout *Salmo trutta* and European grayling *Thymallus thymallus*. The lower area is dominated by iron industry, intensive agriculture and urban areas. In the secondary valleys, the landscape changes to agriculture and forests. The elevation of the valley floor ranges from 458 to 974 masl, with the surrounding mountains up to 1850 masl (Fig. 1).

Large scale habitat suitability

Animal data

The data was provided by Andreas Kranz and colleagues (Kranz & Poledník 2010; Kranz *et al.* 2013). They assessed the density of otters using the method of snow tracking with one-visit-census (Sulkava 2007). For this, a grid layer of 10x10 km was laid over Styria and 33 cells were randomly chosen for snow tracking (Fig. 2). The monitoring was conducted during the winter of 2010/2011, 2011/2012 and 2012/2013, after nights of heavy snowfall to detect tracks along watercourses of a width >1m and all ponds. Tracks were measured and attributed to adult male (single large track), adult female or subadult individual (medium sized track) or female with cubs (medium sized tracks in combination with smaller tracks). Number of adults, subadults and females with cubs were then assigned to each cell.

Environmental data

The large scale HSM was built using the grid with cell size of 10 km^2 identical to the snow tracking census. Based on previous studies on habitat suitability for otters (Ottaviani, Lasinio & Boitani 2004; Remonti *et al.* 2008; Ottaviani *et al.* 2009; Marcelli *et al.* 2012), we used following GIS layers : main river length, length of all watercourses, land cover map and road network (Table 1). The layers were provided by the European Environment Agency (EEA), the GIS office Styria, the Swisstopo institute, Switzerland and Eurostat, Luxembourg. All data were transformed to the same projection (WGS1984, UTM, 33N) before manipulation. As otters move mainly within watercourses and are mostly affected by the immediate surrounding, a buffer of 150 m was created around the river network. Percentages of the three main land cover types (artificial areas, agriculture and closed areas) within this buffer were calculated. All data manipulation and preparation were done using ArcMap software, versions 9.3 and 10 (Environmental Systems Research Institute 2009, 2011).

Analyses

Large cale habitat suitability modelling was conducted using the program MaxEnt version 3.3.3k (http://www.cs.princeton.edu/). Its predictive performance is consistently competitive with the highest performing methods (Elith *et al.* 2009). There were 413 presence locations within the 33 grid cells. Background data was set to 300 cells. Cross validation was maintained in the replicate run and iterations were fixed at 100. Regularization number was set to 1. (see Phillips et al., 2004). Model performance was tested using the AUC (area under the the receiver operation curve ROC), where a perfect fit equals 1, while 0.5 indicates a random model. In addition to this, we used the Jackknife method to assess the importance of variables in the final model (Phillips, Anderson & Schapire 2006).

Fine scale habitat suitability model

Animal data

Between May 2010 to March 2012, 10 otters (three males and seven females) were captured in the fine scale study area and equipped with transmitters (see Chapter 3). Animals were tracked up to four times a week between sunrise and sunset to identify their resting sites (mean=2.41 resting site location/week). When animal was passive, the resting site was identified by homing-in by a single person to an accuracy of <5m. When animals were located in new resting sites, the closest GPS location without disturbing the animal was noted. The location of the animal was calculated in ArcView 3.2 (ESRI 2002). Habitat variables were then attributed to the locations using ArcMap 10. Animals were tracked until the sender failed, the animal disappeared or the field study ended in March 2013. Nine individuals could be tracked more than half a year each and were included in the analyses (mean duration in days = 658, min=252, max=1032). Altogether, the animals were successfully located on 1814 days (mean=208 days, min=65, max=399), excluding the 60 occasions, when individuals could not be found. Altogether, 247 resting sites were found and of which all descriptive data could be sampled. This averaged to 27 resting sites per individual (min=11, max=38).

Environmental data

The naturalness of all main rivers was assessed using the methodology by the Federal office for the Environment FOEN Switzerland (Hütte & Niederhauser 1998). For any given stretch of a river, information was collected on riverbed width, variations in the breadth of the water surface, artificial beds and bank footings and riparian vegetation type and width. Each variable was then weighted using the key provided by Hütte & Niederhauser (1998), resulting in four categories: natural, semi-natural, non-natural and artificial. For any resting site precise ecomorphological information was assigned as well as the overall naturalness for that stretch was assigned (Table 2). As previous studies have shown that otters can perceive roads as disturbance (Chapter 2 and 3), we also calculated the distance to nearest hiking paths, back roads, main roads and a combination of them using ArcGIS 10.

Resource selection was evaluated at the third-order scale within home range (Johnson 1980) and followed a Design III protocol, where availability was sampled for each individual and compared to used resting sites (Manly *et al.* 2002). Availability for otters was calculated by estimating home ranges using fixed kernels (see Chapter 2). Availability was then further restricted to the bank sides of the main riverbeds only, as shown in earlier studies on habitat selection of resting otters (Chapter 3). For each known resting site of an animal, 10 random locations were used within its home range. Environmental data was then attributed to all known and random locations using ArcGIS 10.

Analyses

All continuous covariates were centered and scaled to obtain a mean of 0 and a variance of 1. A standard logistic regression model was then fitted with a binary response variable as indicator if the location was available (0) or used (1). All variables were first included as fixed effects only and the model with the lowest AICc was selected. A Resource selection function (RSF) was then built using the formula

$$RSF = w(x) = exp(\beta_1 x_1 + \ldots + \beta_n x_n),$$

where $x = x_1, \ldots, x_n$ are the predictor covariates. For any values of the covariates x, w(x) corresponds to the respective proportion between the used and the available frequency (f_u /f_a), and reflects the preference for a habitat with covariates x compared to its availability. Values of w(x) > 1 thus represent habitats that are over-proportionally selected by the animal with respect to their availability and w(x) < 1 represents habitats that are avoided.
We then used a k-fold cross-validation to assess model predictions by randomly dividing our sample into five equal-sized subsets with the same number of used and available points to ensure that the 1:1 ratio of used vs. available locations stayed intact. Following Huberty's (1994) rule of thumb, the data was divided into k=5 subsets to obtain a training-to-test ratio of 25%. The coefficients of our best model were re-estimated for each subset. Following Boyce et al. (2002) and the recommendations of Wiens et al. (2008), the predictive capacity of each subset was assessed with Spearman-rank correlations, using ten equal-area bins and a moving-window average for the frequency of cross-validated use locations. For each fold, we used the RSF values of only the available locations in the cross-validated set to determine the borders of the equal-area bins. The window size for the averaging of the frequencies in the bins was chosen to span over five values, namely over the neighbours with distances -2, -1, 0, +1 and +2 (or a respective subset thereof when close to the borders). The resulting correlation values essentially tested if high RSF values indeed predict whether a location is more probable to be used by the animal (Boyce et al., 2002).

Distribution of resting sites within home range

Otters use several resting sites throughout the year. Contrary to other species, the otter is not a central forager but uses several resting sites throughout its home range. Location and distribution of good quality habitat for resting sites may be crucial for the establishment of a territory. For this, all main rivers within each home range were transformed to a network for each individual using the tool “Network analyst” in ArcMap 10. Patchiness of resting site location was then estimated using the GIS-extension SANET 4.1 for ArcMap 10 (Okabe & Okunuki 2015), which analyses events occurring on networks. The underlying hypothesis is the complete spatial randomness (CRS) hypothesis, where the distance from every point in a given set of locations is calculated to the nearest neighbor along the network. A deviation of the observed curve from the expected curve indicates a rejection of the CSR hypothesis with a 0.95 confidence level.

Projection to Switzerland

The model resulting from the data of the tracking study was applied to the area of Switzerland. Here, data on the ecomorphology of over 29 000 km length of watercourses (approx. 70% of all the watercourses of Switzerland) is available (Zeh Weissmann, Könitzer & Bertiller 2009). Maps on the watercourses and roads with a resolution of 1:25 000 were provided by the Swisstopo (Federal office for topography, Wabern, Switzerland), while the FOEN supplied the information on the ecomorphology of the watercourses. We restricted the analysis to the stretches, where information on their naturalness was available. A grid with cell size of 10 km^2 was laid over Switzerland, being identical to the grid of the large scale analysis, thus making a comparison possible. Analysis was done for each cell individually as otherwise the amount of data exceeded the limitations of the computer. For each cell rasters on naturalness and the euclidian distance to roads within a buffer of 5000 m was caluculated at a resolution of 1 m. The resulting rasters were then incorporated in the best model evaluated by the real data from Styria in R 3.2.2 (R Development Core Team, 2015), see above. The output was then back transferred to ArcGIS 10.2. The resolution was then set to 10 m to gain higher visibility and the habitat suitability index was classified in four categories (unsuitable/partly suitable/suitable/optimal). For comparison between the HSM, we calculated the percentage of the best suitability class over all classes for each 10x10 km grid cell. By penalizing each cell with less than 10 km length of watercourse with a weight of 0.5, we acknowledged thus the approximate minimum length of watercourses for home ranges of otters (Chapter 2).

Results

Large scale HSM

The environmental parameters in the model included percentage of the artificial area cover, length of the main river, percentage of agricultural land cover, percentage of closed land cover, percentage of temporary wetlands and density of roads within a buffer of 150 m around the running waters. The model is shown in Fig. 3. The logistic output for current habitat suitability of the Eurasian otter had a rather low success rate. The average test AUC was 0.744, with a standard deviation of 0.181. The percentage of the artificial area cover contributed most to the model (44.4%) with length of the main rivers adding 29%. Closed areas contributed 14.9%, argricultural lands 6.5%, by temporary wetlands 3.3%, while the density of roads added only 2.1%. The output of the jackknife is found in the supplementary information (Fig. S1).

Fine scale habitat suitability

The two best models of resting site selection included the variables “naturalness”, “distance to the nearest road” and the interaction of both variables (for the three models with lowest AICc see Table S1). For both models, the spearman-rank correlation statistics were calculated for 5-fold cross-validation of RSF bin ranks and the frequency of values in the respective bins. The partition into the 5-folds was repeated 100 times and the five resulting rank correlations were stored each time. In average, the best model from model selection process resulted in a slightly lower correlation (0.86, SD = 0.19) than the second best model (0.87, SD = 0.18).

In the best model, resting site locations depended on the interaction of the naturalness and the distance to the nearest road ($p = 0.002$) (Table 3). The selection of resting site depended on the naturalness of the environment ($p < 0.001$), tending in general to be chosen further away from any road (estimate 1.53, $p = 0.07$) than what was available. We then used the estimates of the best model to predict the habitat suitability for otter resting places in Switzerland (Fig. 4). By using the distribution of the resting sites within the habitat suitability map at the study site (Fig. S2a), we then classified the habitat suitability map, ranging from 0-1, into four categories with equal spaced bins (Fig. S2b).

We then overlaid the two HSM for visual comparison (Fig. 5). Additionally, we also calculated the percentage of the best suitability class over all classes for each 10x10 km grid cell, to compare the fine scale HSM with the coarse HSM built on the snow tracking data for Austria (Fig. S3). Fine and coarse scale habitat suitability maps at this resolution show a good fit with the few confirmed otter sightings in Switzerland (www.prolutra.ch, October 2015) but differ largely elsewhere (Fig. S4).

Distribution of locations

In general, clusters of resting sites were observed up to approx. 3000 m but were randomly dispersed at higher distances (Fig. 6). For three individuals, the CSR hypothesis was rejected for any distance (Fig. 6c,f and g).

Discussion

We investigated the habitat suitability for otters at two different scales to predict future otter presence to an area, where the species has been extinct since the late 1980s. The models showed large areas with suitable habitat for otters at both scales, thus indicating that the core of the Alps can be recolonized by otters and a reconnection across Switzerland to the populations of Austria (east), France (west) and Italy (south) is possible based on our models.

Factors influencing the large scale HSM

Percentages of artificial land cover contributed most to the model at the large scale HSM. This is similar to the findings of Robitaille and Laurence (2002). However, we deliberately excluded human density in our models based on two decisions: usability and transferability. Although human density is considered to have a negative effect on otter presence (Robitaille & Laurence 2002; Clavero *et al.* 2010), otters have turned up recently in areas with high human density (Kranz & Toman 2000; Kloskowski, Rechulicz & Jarzynowa 2013). This can question the reliability of human density as a predictor for areas where otters are still extinct. The current occurrence of a species can be strongly linked to recent distribution, dispersal abilities and local habitat permeability, while less so to large scale environmental factors (Radinger & Wolter 2015). Although otters cover large territories (e.g. Erlinge 1967), their willingness to disperse seems limited (Quaglietta *et al.* 2013). Thus habitat suitability at large scale might not solely responsible for current otter distribution as suggested already in an earlier study (Remonti *et al.* 2008). Additionally, human density is generally higher in Switzerland than Styria. Thus, by excluding this variable, we avoided an intrinsic bias. However, humans can be perceived as disturbances for otters (Chapters 2 & 3). We therefore incorporated the spatial distribution of humans within a buffer of 150 m to the watercourses by using density of roads, which has been shown to increase with the number of buildings (Hawbaker *et al.* 2004). Complementary, we used the land cover class “artificial” as a proxy for the anthropogenic impact on the watercourses because artificial surfaces along watercourses have negative impact on the freshwater ecosystem and its biodiversity (Urban *et al.* 2006). This land cover class is linked to human presence, but it does not mirror population density (Gallego 2004). Lakes are known to be suitable habitat for otters (Kruuk 2006). However, the incorporation of lakes to the large scale HSM would have biased the results as there are no large lakes in Styria. By excluding this variable, we reduced the potential of occurrence in the cells with lakes in Switzerland, but did not overestimate the avoidance due to the differences between the regions.

Factors influencing the fine scale HSM

At the fine scale, otters selected resting sites depending on the naturalness and the distance to the nearest road. We focused on the resting site selection because resting behavior has been shown to be the behavior which demands higher requirements of the environment at the fine scale level (Chapter 2 & 3). While otters use their habitat opportunistically for foraging (Chapter 2), suitable habitat for resting sites could be a limiting factor as shown in other species (Birks, Messenger & Halliwell 2005; Batavia *et al.* 2010; Lutermann, Verburgt & Rendigs 2010). Indeed, otters sleep almost exclusively in the riparian vegetation (Chapter 3), which belongs to the most degraded and threatened ecosystems worldwide (Millenium Ecosystem Assessment 2005).

Vegetation cover has a protective function for carnivores in anthropogenic landscapes (Ordiz *et al.* 2011; Fernandez-Lopez *et al.* 2014; Sálek *et al.* 2014). Also otters rely on the riparian vegetation as a protection against human disturbance (Chapter 3). Within the riparian vegetation belt, resting sites of otters can be situated above ground in structures such as stick piles, in dense vegetation and in underground burrows such as cavities in the root system and boulders (Green, Green & Jefferies 1984; Ruiz Olmo, Jimenez & Lopez Martin 1995; Beja 1996). In the Alpine Arc, many of cavities used by otters can be found in revetments along watercourses (Freire 2011; Weinberger, unpublished), indicating a flexibility in accepting novel habitat structures created by man. It also explains the strong positive effect of semi-natural and even non-natural stretches to the model (see Fig. S5). Alternatively, a potential explanation could be the riparian maintenance, which is more intense along stretches with better access. Riparian maintenance may lead to a higher abundance of stick piles, from which otters benefit. Thus, there is most likely some trade-off between the availability of resting site structures and human disturbance, which could result in a bimodal distribution. However, this was not detected at this scale.

Environmental data on the freshwater ecosystems is often restricted in extent, locally and informatively, hampering the comparison between the study areas. However, by implementing a methodology already applied to over 70% of the watercourses in Switzerland to the radiotracking study area yielded comparable environmental data. The limitation of the assessment exclusively to the main riverbeds can be justified with the ranging behavior of otters, which was mostly restricted to main watercourses (Chapter 2 & 3).

Limitations of the HSMs

Besides habitat factors, prey abundance and pesticides may influence otter occurrence and persistence (Ruiz-Olmo *et al.* 2011; Pountney *et al.* 2014). Data on those aspects proved difficult to obtain for the study areas at any scale, making a comparison impossible. The presence of pesticides and a low prey availability will negatively affect otter presence. Swiss fish populations have declined seriously in recent years, with decreases of 30% and more (Burkhardt-Holm, Peter & Segner 2002). Therefore, by omitting fish biomass, we certainly overestimated habitat suitability for otters. A further development of the present HSMs with implementation of prey biomass and environmental pollutants is thus highly encouraged.

We are also aware of the low habitat suitability along the edge of the study areas at the large scale HSM. The national borders run through those cells, with only reduced information on environmental parameters such as river lengths or density of roads. The environmental data for those cells from the respective country (e.g. France, Italy, Germany) would mitigate the problem of this edge effect.

Implications of the distribution of resting sites

Otters have several resting sites, distributed throughout their home ranges. Little is known of the resting site distribution of carnivores in relation to their territory. While habitat preferences are crucial for resting site selection (Theuerkauf, Rouys & Jedrzejewski 2003; Larroque *et al.* 2015), its has been suggested that patches of food resources could influence spatial distribution of resting sites (Joshi, Smith & Cuthbert 1995). Location of good foraging habitat may explain the distribution of resting sites of otters. Additionally, the clustering of the resting sites could be attributable to the degradation of resting sites over time, differences in microclimate among resting sites or avoidance behaviour to parasites. On several occasions, otters of opposite sex were observed to sleep in the same resting site or in resting sites in close proximity (pers. obs. Irene Weinberger). Thus, the occurrence of a cluster of resting sites could also be an indicator of social interactions.

The importance of the scale

Fine and large scale HSM differ quite substantially. Little information on riverine landscape is available for large areas. Indeed, watercourses are usually just small bands running through the landscape and their riparian vegetation goes unnoticed at a large scale resolution. However, it is exactly this belt, which influences the whole freshwater ecosystem. Thus, large scale variables such as agricultural fields or artificial grounds by CORINE land cover may not precisely mirror the state of the watercourse and its immediate surrounding. Fine scale HSM may capture the state of the watercourses much more precisely, but will fail where no data is available. But even here, the resolution may be too coarse. First, resting sites can be on both sides of a watercourse. This has been neglected here as we used the ecomorphological classification, which covers both sides. Additionally, human disturbance along watercourses will most likely contribute substantially to the availability of resting sites. Otters seem to prefer areas with low human activity or need natural riparian vegetation cover as a protective buffer against human disturbance. Those hiking trails are often unmarked on maps and intensity of their use by humans is unknown. Thus, the fine scale HSM here may actually overestimate habitat suitability in many areas. Close observation of the ongoing expansion of the otter populations will yield more insights into the hierarchy of the different scales. Indeed, otter sightings have been reported to Switzerland in the last few years (www.prolutra.ch), but are located in areas with suitable habitat at both scales. Our work demonstrates the importance of scales and the need to address habitat suitability at different scales as shown by du Toit (2010).

Connectivity

One of the fundamental aspects of a natural re-expansion of a species is the permeability of the landscape matrix. In our work, we did not address connectivity of the landscape as this has been done before for the core of the Alps (Cianfrani *et al.* 2013). The outcome of that study showed a high permeability to the surrounding populations as well as a high structural connectivity within Switzerland. The structural connectivity (availability of corridors) may differentiate from the functional connectivity, which defines the used corridors. Thus, fine scale obstacles could pose a problem, e.g. dispersal over roads with high volume of traffic. Road mortality can be detrimental for the development on an expanding population (Kramer Schadt *et al.* 2004). Indeed, traffic has been shown to be a major cause for mortality in otters (Philcox, Grogan & Macdonald 1999; Guter *et al.* 2006; Bjorklund & Arrendal 2008), thus a further detailed investigation on potential local impediments may further facilitate recovery of the species and the interconnection of the nowadays expanding populations in France and Austria.

Conclusions

Using a multi-national approach, we predicted habitat suitability at two different scales for Switzerland. Situated at the core of the Alpine Arc, Switzerland is central for the reconnection of the otter populations in the surrounding countries. Even though the Alpine Arc is one of the last pristine landscapes in central Europe, habitat suitability for otters can be limited as the valley bottoms within the Alps have been modified in large parts for human use, e.g. roads, hydropower and intensification of agriculture. Indeed, anthropogenic changes to the freshwater ecosystem most likely shapes the recovery of the species.

The HSMs built in this study give insights at the national and regional level and can be used as contribution to facilitate and mitigate otter recovery. Both HSMs predicted suitable habitat for otters in Switzerland. The large-scale HSM showed a strong negative influence of human dominated landscapes, while at the fine scale, otters seem to tolerate modifications to the watercourses. However, habitat selection at an even finer resolution indicated that resting otters perceive humans as threats and select the locations of their resting sites depending on expected human presence (Chapter 3). This demonstrates the importance of investigating animal behavior at the finest possible scales to be able to incorporate the habitat requirements at that scale. As information on the quantity of human activities is unavailable for most paths, a stepwise top-down approach may be successful in otter conservation.

Besides habitat variables and human densities, fish biomass as well as environmental pollutants may play an important role. Further research to investigate prey availability and the amount of pollutants is encouraged.

References

92/43/EEC. (1992) Conservation of Natural Habitats and of Wild Fauna and Flora.

Araújo, M.B. & Williams, P.H. (2000) Selecting areas for species persistence using occurrence data. *Biological Conservation*, **96**, 331–345.

Batavia, M., Matsushima, A., Eboigboden, O. & Zucker, I. (2010) Influence of pelage insulation and ambient temperature on energy intake and growth of juvenile Siberian hamsters. *Physiology & behavior*, **101**, 376–380.

Beja, P.R. (1996) Temporal and spatial patterns of rest-site use by four female otters Lutra lutra along the south-• west coast of Portugal. *Journal of Zoology*, **239**, 741–753.

Birks, J.D.S., Messenger, J.E. & Halliwell, E.C. (2005) Diversity of den sites used by pine martens Martes martes: A response to the scarcity of arboreal cavities? *Mammal Review*, **35**, 313–320.

Bjorklund, M. & Arrendal, J. (2008) Demo-genetic analysis of a recovering population of otters in Central Sweden. *Animal Conservation*, **11**, 529–534.

Burkhardt-Holm, P., Peter, A. & Segner, H. (2002) Decline of fish catch in switzerland: Project fishnet: A balance between analysis and synthesis. *Aquatic Sciences*, **64**, 36–54.

Cabeza, M., Arponen, A., Jäättelä, L., Kujala, H., van Teeffelen, A. & Hanski, I. (2010) Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54–63.

Carone, M.T., Guisan, A., Cianfrani, C., Simoniello, T., Loy, A. & Carranza, M.L. (2014) A multi-temporal approach to model endangered species distribution in Europe. The case of the Eurasian otter in Italy. *Ecological Modelling*, **274**, 21–28.

Carranza, M.L., D'Alessandro, E., Saura, S. & Loy, A. (2012) Connectivity providers for semi-aquatic vertebrates: The case of the endangered otter in Italy. *Landscape Ecology*, **27**, 281–290.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V. & Adamec, M. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**, 1517–1519.

Cianfrani, C., Lay, L., Hirzel, A.H., Loy, A. & Le Lay, G. (2010) Do habitat suitability models reliably predict the recovery areas of threatened species? *Journal of Applied Ecology*,

47, 421–430.

Cianfrani, C., Lay, G. Le, Maiorano, L., Satizábal, H.F., Loy, A. & Guisan, A. (2011) Adapting global conservation strategies to climate change at the European scale: The otter as a flagship species. *Biological Conservation*, **144**, 2068–2080.

Cianfrani, C., Maiorano, L., Loy, A., Kranz, A., Lehmann, A., Maggini, R. & Guisan, A. (2013) There and back again? Combining habitat suitability modelling and connectivity analyses to assess a potential return of the otter to Switzerland. *Animal Conservation*, **16**, 584–594.

Clapham, P.J., Young, S.B. & Brownell, R.L. (1999) Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Review*, **29**, 37–62.

Clavero, M., Blanco-Garrido, F. & Prenda, J. (2005) Fish-habitat relationships and fish conservation in small coastal streams in southern Spain. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**, 415–426.

Clavero, M., Hermoso, V., Brotons, L. & Delibes, M. (2010) Natural, human and spatial constraints to expanding populations of otters in the Iberian Peninsula. *Journal of Biogeography*, **37**, 2345–2357.

Collingham, Y.C., Wadsworth, R.A., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of non-indigenous riparian weeds: Issues of spatial scale and extent. *Journal of Applied Ecology*, **37**, 13–27.

Le Corre, M., Danckwerts, D.K., Ringler, D., Bastien, M., Orlowski, S., Morey Rubio, C., Pinaud, D. & Micol, T. (2015) Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island, western Indian Ocean. *Biological Conservation*, **185**, 85–94.

Cortés, Y., Fernández-Salvador, R., García, F.J., Virgós, E. & Llorente, M. (1998) Changes in otter Lutra lutra distribution in Central Spain in the 1964-1995 period. *Biological Conservation*, **86**, 179–183.

Elith, J., Graham, C.H., Anderson, R.P., Duik, M., Ferrier, S., Gsuian, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Philips, S.., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Sobero’n, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2009) Novel methods improve prediction of species’ distributions from occurrence data. *Ecography*, **29**.

Erlinge, S. (1967) Home range of the otter Lutra lutra L. in southern Sweden. *Oikos*, **18**, 186–209.

ESRI. (2009) ArcGis Desktop: Release 9.3.

ESRI. (2011) ArcGIS Desktop: Release 10.

Fernandez-Lopez, J., Fandos, G., Cano, L.S., Garcia, F.J. & Telleria, J.L. (2014) Effect of wildlife refuges on small carnivores in a hunting area in Mediterranean habitat. *Hysterix*, **25**, 45–46.

Foster-Turley, P., Macdonald, S.M. & Mason, C.F. (1990) *Otters: An Action Plan for Their Conservation*. IUCN Otter Specialist Group.

Freire, S.I. (2011) *Day Resting Site Use and Fidelity of Alpine Otters (Lutra Lutra) in Southeast Austria*. Master thesis. University of Lisbon.

Gallego, F.J. (2004) Mapping rural / urban areas from population density grids. , 1–19.

Green, J., Green, R. & Jefferies, D.J. (1984) A radio-tracking survey of otters Lutra lutra on a Perthshire river system. *Lutra*, **27**, 85–145.

Guter, A., Dolev, A., Saltz, D. & Kronfeld-Schor, N. (2006) Temporal and spatial influences on road mortality in otters: Conservation implications. *Israel Journal of Zoology*, **51**, 199–207.

Hawbaker, T.J., Radeloff, V.C., Hammer, R.B. & Clayton, M.K. (2004) Road density and landscape pattern in relation to housing density, and ownership, land cover, and soils. *Landscape Ecology*, **20**, 609–625.

Hutson, A.M., Mickleburth, S.P. & Racey, P.A. (2001) *Microchiropteran Bats: Global Stauts Survey and Conservation Action Plan*.

Hütte, M. & Niederhauser, P. (1998) *Methoden zur Untersuchung und Beurteilung der Fliessgewässer in der Schweiz. Ökomorphologie Stufe F (flächendeckend)*. Bern.

Institute, E.S.R. (2002) ArcView 3.2.

Janssens, X., Defourny, P., Kermabon, J. De & Baret, P. V. (2006) The recovery of the otter in the Cevennes (France): a GIS-based model. *Hystrix*, **17**, 5–14.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Joshi, A.R., Smith, J.L. & Cuthbert, F.J. (1995) Influence of food distribution and predation pressure on spacing behavior in palm civets. *Journal of Mammalogy*, **76**, 1205–1212.

Kemenes, I. & Demeter, A. (1995) A predictive model of the effect of environmental factors on the occurrence of otters (Lutra Lutra L.) in Hungary. *Hystrix*, **7**, 209–218.

Klenke, R. (1998) Habitat suitability and apparent density of the Eurasian otter (Lutra lutra) in Saxony (Germany). *IUCN Otter Specialist Group Bulletin*, **19**, 167–171.

Kloskowski, J., Rechulicz, J. & Jarzynowa, B. (2013) Resource availability and use by Eurasian otters Lutra lutra in a heavily modified river-canal system. *Wildlife Biology*, **19**, 439–451.

Kramer Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004) Fragmented landscapes, road mortality and patch connectivity: Modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, **41**, 711–723.

Kranz, A. (2000) Otters (Lutra lutra) increasing in Central Europe: From the threat of extinction to locally perceived overpopulation? *Mammalia*, **64**, 357–368.

Kranz, A. & Poledník, L. (2010) *Quantifizierung von Fischottern bei Neuschnee Quadraten der Ostalpen*. Chur, Switzerland.

Kranz, A. & Poledník, L. (2015) *Fischotter in Kärnten: Verbreitung & Bestand 2014*. Graz.

Kranz, A., Polednik, L., Pavanello, M. & Kranz, I. (2013) *Fischotterbestand in der Steiermark - Spurschneekartierungen 2010 - 2013. Endbericht.* Graz, Austria.

Kranz, A. & Toman, A. (2000) Otters recovering in man-made habitats in central Europe. *Mustelids in a modern world*, Huw I. Gri (ed H.I. Griffiths), pp. 163–184. Bachhuys Publishers, Leiden, Netherlands.

Kruuk, H. (2006) *Otters: Ecology, Behaviour and Conservation*. Oxford University Press Inc., New York.

Larroque, J., Ruette, S., Vandel, J.-M. & Devillard, S. (2015) Where to sleep in a rural landscape? A comparative study of resting sites pattern in two syntopic Martes species. *Ecography*, **38**, 1–12.

Van Looy, K., Cavillon, C., Tormos, T., Piffady, J., Landry, P. & Souchon, Y. (2013) A scale-sensitive connectivity analysis to identify ecological networks and conservation value in river networks. *Landscape Ecology*, **28**, 1239–1249.

Loy, A., Carranza, M., Cianfrani, C., D'Alessandro, E., Bonesi, L., Di Marzio, P., Minotti, M. & Reggiani, G. (2009) Otter Lutra lutra population expansion: Assessing habitat suitability and connectivity in southern Italy. *Folia Zoologica*, **58**, 309–326.

Lutermann, H., Verburgt, L. & Rendigs, A. (2010) Resting and nesting in a small mammal: Sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*, **79**, 1211–1219.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Seletion by Animals*, 2nd Edition. Kluwer Academic Publishers,Dordrecht, Netherlands.

Marcelli, M. & Fusillo, R. (2009) Assessing range re-expansion and recolonization of human-impacted landscapes by threatened species: a case study of the otter (Lutra lutra) in Italy. *Biodiversity and Conservation*, **18**, 2941–2959.

Marcelli, M., Poledník, L., Poledníková, K. & Fusillo, R. (2012) Land use drivers of species re-expansion: inferring colonization dynamics in Eurasian otters. *Diversity and Distributions*, **18**, 1001–1012.

Mason, C.F. & MacDonald, S.M. (1986) *Otters: Ecology and Conservation*. Cambrige University Press, New York.

McAlpine, C.A., Rhodes, J.R., Callaghan, J.G., Bowen, M.E., Lunney, D., Mitchell, D.L., Pullar, D. V. & Possingham, H.P. (2006) The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: A case study of koalas in Queensland, Australia. *Biological Conservation*, **132**, 153–165.

Millenium Ecosystem Assessment. (2005) *Ecosystems and Human Well-Being: Wetlands and Water Synthesis*. Washington.

Musiani, M. & Paquet, P. (2004) The Practices of Wolf Persecution, Protection, and Restoration in Canada and the United States. *BioScience*, **54**, 50–60.

Okabe, A. & Okunuki, K. (2015) SANET - A Spatial Analysis along Networks (Ver.4.1).

Ordiz, A., Stoen, O.-G., Delibs, M. & Swenson, J.E. (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**, 59–67.

Ottaviani, D., Lasinio, G.J. & Boitani, L. (2004) Two statistical methods to validate habitat suitability models using presence-only data. *Ecological Modelling*, **179**, 417–443.

Ottaviani, D., Panzacchi, M., Jona Lasinio, G., Genovesi, P., Boitani, L., Lasinio, G.J. & Jonalasinio, G. (2009) Modelling semi-aquatic vertebrates' distribution at the drainage basin scale: The case of the otter Lutra lutra in Italy. *Ecological Modelling*, **220**, 111–121.

Ottino, P., Prigioni, C. & Taglianti, V. (1995) Habitat suitability for the otter (Lutra lutra) of some rivers of Abruzzo region (central Italy). *Hysterix*, **7**, 265–268.

Parry, G.S., Bodger, O., McDonald, R.A. & Forman, D.W. (2013) A systematic re-sampling approach to assess the probability of detecting otters Lutra lutra using spraint surveys on small lowland rivers. *Ecological Informatics*, **14**, 64–70.

Philcox, C.K., Grogan, a. L. & Macdonald, D.W. (1999) Patterns of otter Lutra lutra road mortality in Britain. *Journal of Applied Ecology*, **36**, 748–761.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Poiani, K.A., Richter, B.D., Anderson, M.G. & Richter, H.E. (2000) Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks. *BioScience*, **50**, 133.

Pountney, A., Filby, A.L., Thomas, G.O., Simpson, V.R., Chadwick, E. A, Stevens, J.R. & Tyler, C.R. (2014) High liver content of polybrominated diphenyl ether (PBDE) in otters (Lutra lutra) from England and Wales. *Chemosphere*, **118C**, 81–86.

Prigioni, C. (1995) Guidelines for the feasibility study of reintroduction of the otter Lutra lutra in Italy: the project of the Ticino Valley (North-Western Italy). *Hystrix*, **7**, 255–264.

Prigioni, C., Remonti, L., Smiroldo, G., Balestrieri, A. & Reggiani, G. (2008) Surveying otter lutra lutra distribution at the southern limit of its italian range. *Hystrix*, **19**, 165–173.

Quaglietta, L., Fonseca, V.C., Hájková, P., Mira, A. & Boitani, L. (2013) Fine-scale population genetic structure and short-range sex-biased dispersal in a solitary carnivore, Lutra lutra. *Journal of Mammalogy*, **94**, 561–571.

Radinger, J. & Wolter, C. (2015) Disentangling the effects of habitat suitability, dispersal, and fragmentation on the distribution of river fishes. *Ecological Applications*, **25**, 914–927.

Remonti, L., Prigioni, C., Balestrieri, A., Sgrosso, S. & Priore, G. (2008) Distribution of a recolonising species may not reflect habitat suitability alone: The case of the Eurasian otter (Lutra lutra) in southern Italy. *Wildlife Research*, **35**, 798–805.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484.

Robbins, M.M., Gray, M., Fawcett, K.A., Nutter, F.B., Uwingeli, P., Mburanumwe, I., Kagoda, E., Basabose, A., Stoinski, T.S., Cranfield, M.R., Byamukama, J., Spelman, L.H. & Robbins, A.M. (2011) Extreme conservation leads to recovery of the virunga mountain gorillas. *PLoS ONE*, **6**.

Robitaille, J.F. & Laurence, S. (2002) Otter, Lutra lutra, occurrence in Europe and in France in relation to landscape characteristics. *Animal Conservation*, **5**, 337–344.

Ruiz Olmo, J., Jimenez, J. & Lopez Martin, J.M. (1995) Radio-tracking of otters Lutra lutra in north-eastern Spain. *Lutra*, **38**.

Ruiz-Olmo, J., Batet, A., Mañas, F. & Martínez-Vidal, R. (2011) Factors affecting otter (Lutra lutra) abundance and breeding success in freshwater habitats of the northeastern Iberian Peninsula. *European Journal of Wildlife Research*, **57**, 827–842.

Ruiz-Olmo, J., López-Mart, J.M. & Palazón, S. (2001) The influence of fish abundance on the otter (Lutra lutra) populations in Iberian Mediterranean habitats. *Journal of Zoology, London*, **254**, 325–336.

Rushton, S.P., Merod, S.J.O.R. & Kerby, G. (2004) New paradigms for modelling species distributions ? *Journal of Applied Ecology*, **41**, 193–200.

Sálek, M., Cervinka, J., Pavluvˇ, P., Poláková, S. & Tkadlec, E. (2014) Forest-edge utilization by carnivores in relation to local and landscape habitat characteristics in central European farmland. *Mammalian Biologie - Zeitschrift fuer Saeugetierkunde*, **79**, 176–182.

Sulkava, R. (2007) Snow tracking: a relevant method for estimating otter Lutra lutra populations. *Wildlife Biology*, **13**, 208–218.

R Development Core Team (2015) A language and environment for statistical computing. R Foundation for Statistical Computing.

Temple, H.J. & Terry, A. (2007) *The Status and Distribution of European Mammals*. Office for Official Publications of the European Communities, Luxembourg.

Theuerkauf, J., Rouys, S. & Jedrzejewski, W. (2003) Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. *Canadian Journal of Zoology*, **81**, 163–167.

du Toit, J.T. (2010) Considerations of scale in biodiversity conservation. *Animal*

Conservation, **13**, 229–236.

Urban, M.C., Skelly, D.K., Burchsted, D., Price, W. & Lowry, S. (2006) Stream communities across a rural – urban landscape gradient. *Diversity and Distributions*, **12**, 337–350.

Wakonigg, H., Hawranek, V., Podesser, A. & Rieder, H. (2010) Temperatur. *Klimaatlas Steiermark - Periode 1971-2000. Eine anwenderorientierte Klimatographie* (eds F. Prettenthaler, A. Podesser, & H. Pilger), pp. 4–145. Verlag der oesterreichischen Akademie der Wissenschaften, Vienna, Austria.

Weber, D. (1990) *Das Ende des Fischotters in der Schweiz - Schlussbericht der 'Fischottergruppe Schweiz' 1984-1990*. Bundesamt für Umwelt, Wald und Landschaft, Bern.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.

Woodroffe, R. (2000) Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation, **3**, 165–173.

Zeh Weissmann, H., Könitzer, C. & Bertiller, A. (2009) *Strukturen der Fliessgewässer in der Schweiz. Zustand von Sohle, Ufer und Umland (Oekomorphologie); Ergebnisse der oekomorphologischen Kartierung.* Bern, Switzerland.

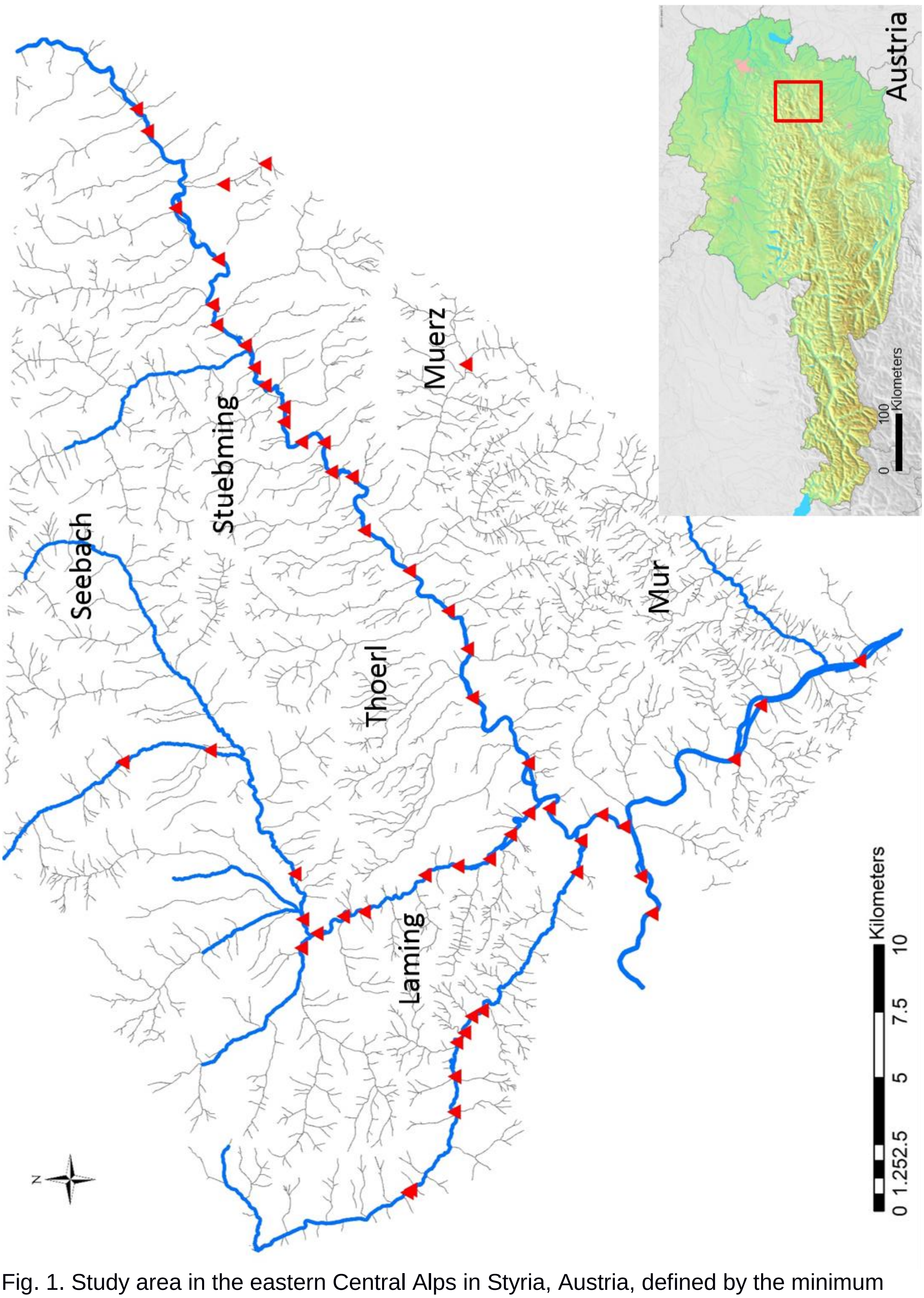


Fig. 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters showing the running and standing water bodies. Blue = watercourses ≥4m, grey= streams <4m. Red triangles=reservoir dams (n=55).

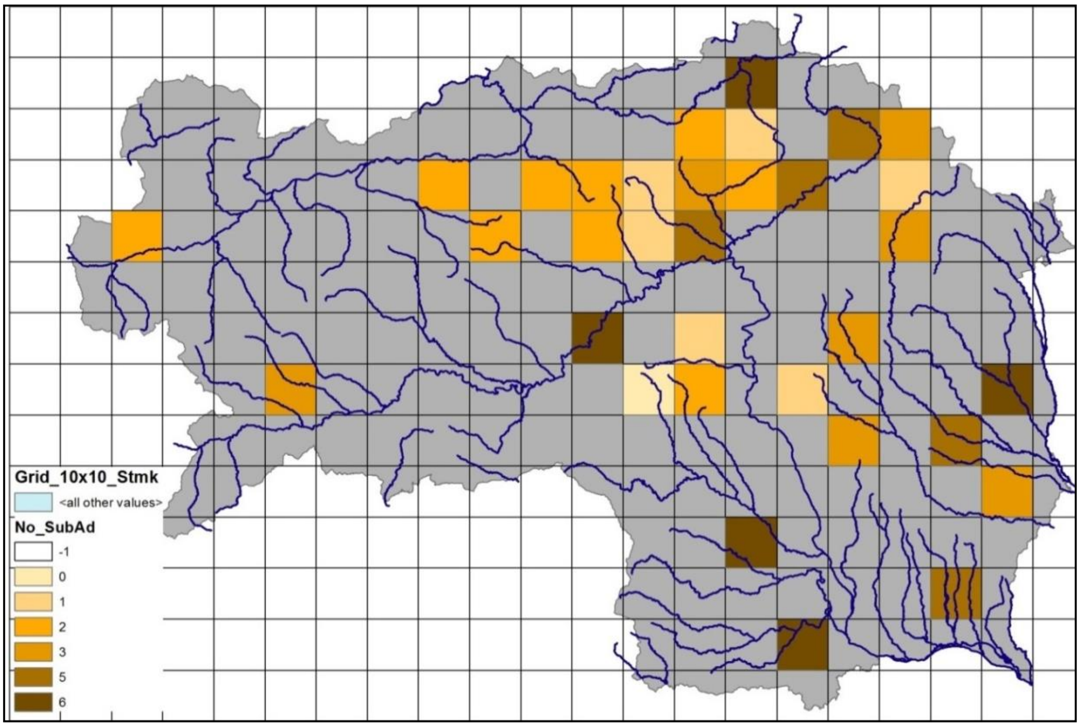


Fig. 2. Snow tracking data. Coloured cells were monitored, unsurveyed cells are grey. The darker the colour, the more adult or subadult individuals were tracked. Figure adapted from Kranz et al 2013.

Fig. 3. Habitat suitability map based on data from snow tracking surveys in Styria. The darker the cell, the higher the suitability. Please note that the low suitability along the edges of both areas is due to the edge effect.

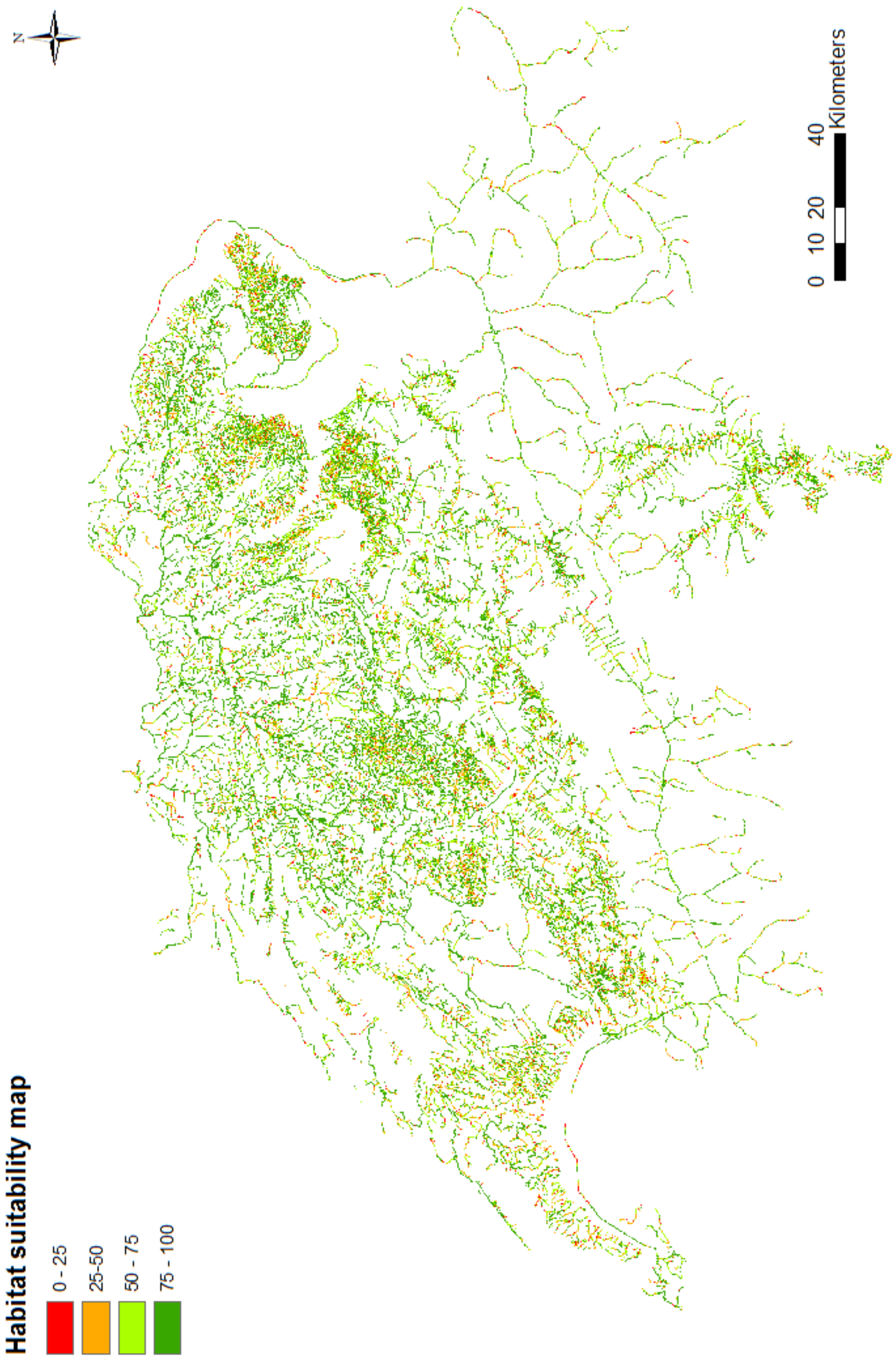


Fig. 4. Habitat suitability map of Switzerland. All watercourses > 4m here are included, but only where the ecomorphological assessment had been available. The number of watercourses assessed differs among Cantons, resulting in patchy distribution of riverine networks.

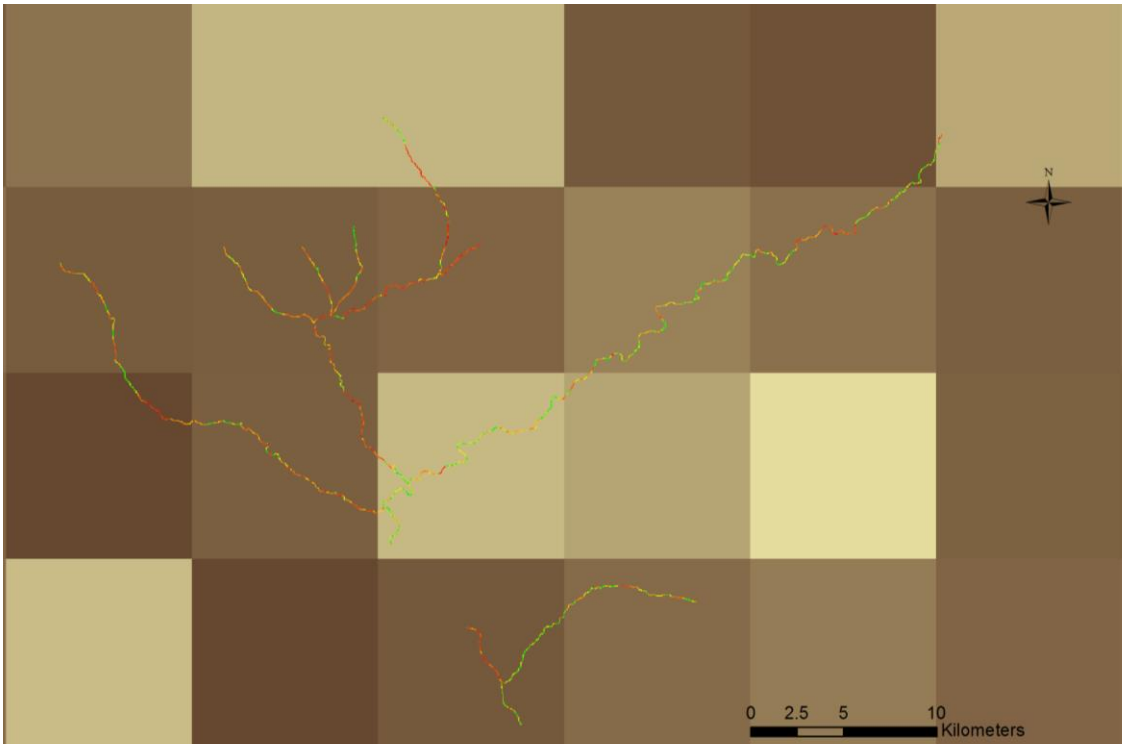


Fig. 5. Combination of the two habitat suitability models at different scales. Grid cells belong to the coarse HSM at 10 km^2 resolution. Habitat suitability increases with color darkness. The fine scale HSM is shown as watercourses. Green stretches signify suitable habitats; yellow = good habitat; orange = suboptimal habitat, red = unsuitable habitat.

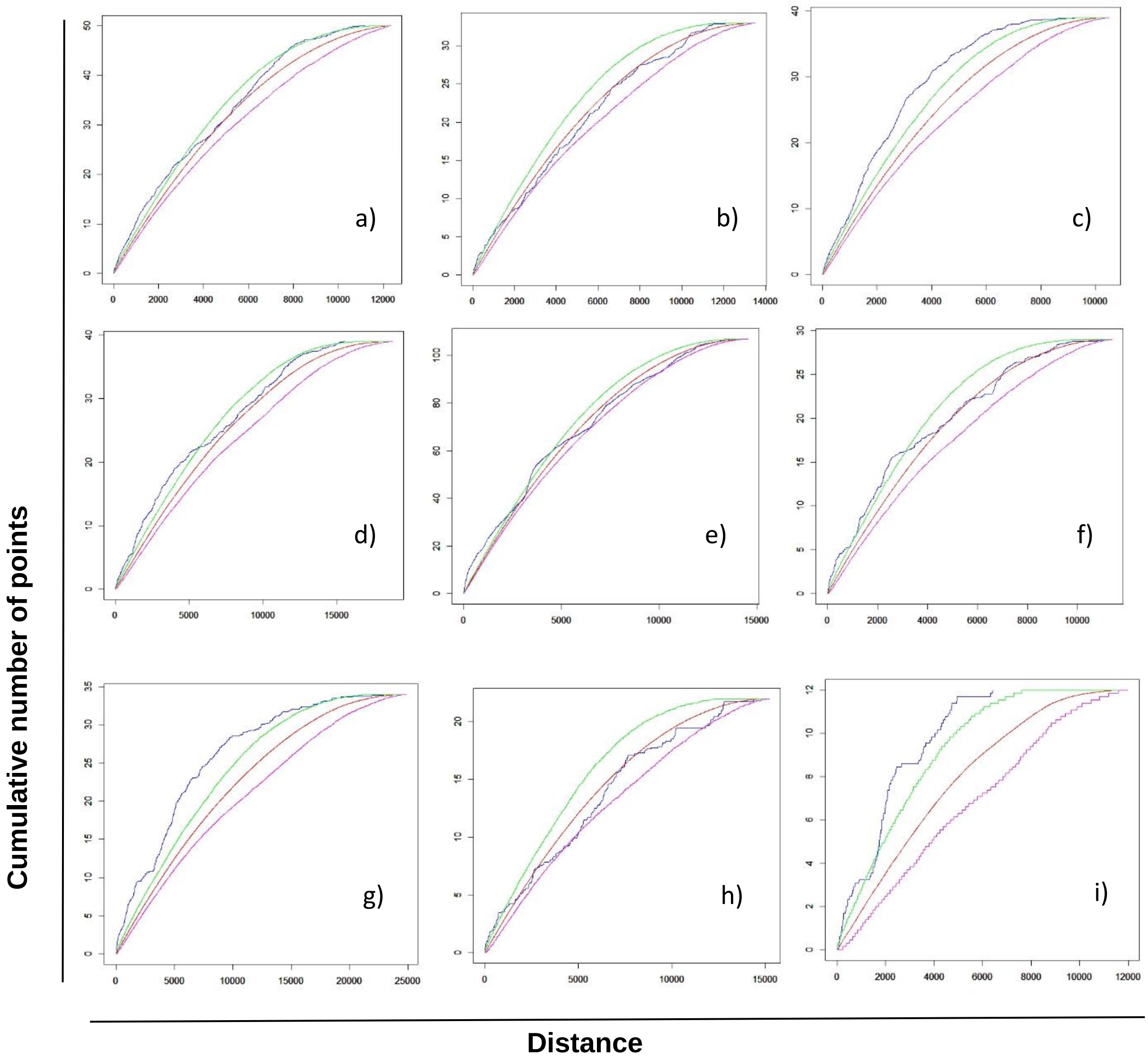


Fig. 6. Distribution of resting sites within the home ranges of the nine radiotracked animals (a-i). The red curve indicates the mean value under the complete spatial randomness hypothesis. The blue line indicates the true values. If the observed curve is in between the upper and lower confidence interval, the CSR hypothesis cannot be rejected.

Table 1. Environmental variables used for large scale habitat suitability including origin.

Variables	Origin Austria	Origin Switzerland
Running waters	Rivernetwork 1:50'000	Rivernetwork (only surface water) 1:25'000
Hiking paths	Styria GIS office	Swisstopo
Landcover 150m	EEA	EEA
Standing waters	Styria GIS Office	Swisstopo
Human density	EEA	EEA

Data Layer	Symbol in Text	Description
HG_Riverlength	HG_Riverlength	River length of main rivers only
All Riverlengths		
Density of Hiking and Cycling paths	Dens_WaRa	Density of Hiking and cycling paths within 10 km grid
Landcover within a buffer of 150m around the running waters		
Artificial areas	*V1*	*Urban areas, mines, artifical greens*
Agriculture	*V2*	*Agricultural areas including meadows*
Closed areas	*V3*	*Forests, shrubs and open natual areas with low vegetation*
Temporary waterbodies	*V4*	*marsh, moors*
Human density		
Paved Roads		
Paved roads length	CHAT_PavedRoads150	Length of Paved roads within 150m of the river
Paved roads density	chat_denspavroad150m.asc	Denstiy of Paved roads within 150m of the river
Standing waters	CHAT-	

Table 2. Habitat and disturbance variables used in the analyses. The variables indicated with a star are used for the classification for naturalness (see Hütte & Niederhauser 1998 for more information).

Variables	Code	Description	Measurement
River bed width*	RWIDTH	Width of the running water	Continuous in meters
Variation in bed width*	VAR	Variation in the breadth of the water surface	Ordinal (1-3, with 1=large variabilty, 2=constricted and 3 = none)
Bed modification*	MBED	The extent to which the bed has been modified (e.g. concrete floor)	Ordinal (1-6, with 1=no modification, 2=<10%, 3=10-30%, 4<30%, 5<50%, 6=complete)
Type of bed modification*	TBED	Type of material used for the bed modification	Categories (1-5, with 1=loose stones, 2=wood, 3=stones made of concrete, 4=impermeable, 5=others)
Bank modification*	MBANK	The extent to which the bank side has been modified (e.g. stones along the bank for flood prevention)	Ordinal (1-6, with 1=no modification, 2=<10%, 3=10-30%, 4<30%, 5<50%, 6=complete)
Type of bank modification*	TBANK	The permeability between the river bed and the bank side (e.g.for water or detritus)	Ordinal (1-2, with 1=permeable, 2=impermeable)
Vegetation width*	VWIDTH	Width of natural or semi-natural vegetation measured from waterside	Continuous in meters
Vegetation type	VTYPE	Type of vegetation from the river perspective: natural (forest, reed, herbacous stretches with at least 1 tree/bush within 25m), foreign (herbacous, meadow, grass), artifical (none)	Ordinal (1-3, with 1=natural, 2=foreign and 3 = artificial)
Distances			
to hiking paths	DistPATH	Distance to hiking paths within 2000m to the water	Continuous in meters
to secondary roads	DistPaRo	Distance to paved roads that are not main roads within 2000m to the water	Continuous in meters
To main roads	DistR	Distance to all main roads within 2000m	Continuous in meters
to roads combined	DistR_ALL	Distances to all roads and hiking paths combined within 2000m	Continuous in meters

Table 3. Summary of the best model selected for selection of resting sites at the fine scale. Variables in italics show the overall value (including the reference category) of the term in the model (chi-square value).

Variables	**Estimate**	**Std. Error**	**z value**	**P value**
Naturalness				< 0.0001
Semi-natural (p=0.2)	1.32	1.03	1.27	0.2
Non natural (p=0.36)	0.94	1.03	0.91	0.36
Artifical (p=0.08)	0.26	1.05	0.26	0.8
Distance to roads	1.53	0.85	1.82	0.07
Naturalness : Distance to roads				0.00188
Semi-natural:Distance to roads (p=0.06)	-1.62	0.85	-1.91	
Non natural: Distance to roads (p=0.18)	-1.13	0.85	-1.34	
Artifical:Distance to roads (p=0.18)	-1.16	0.85	-1.34	

Supplementary Information

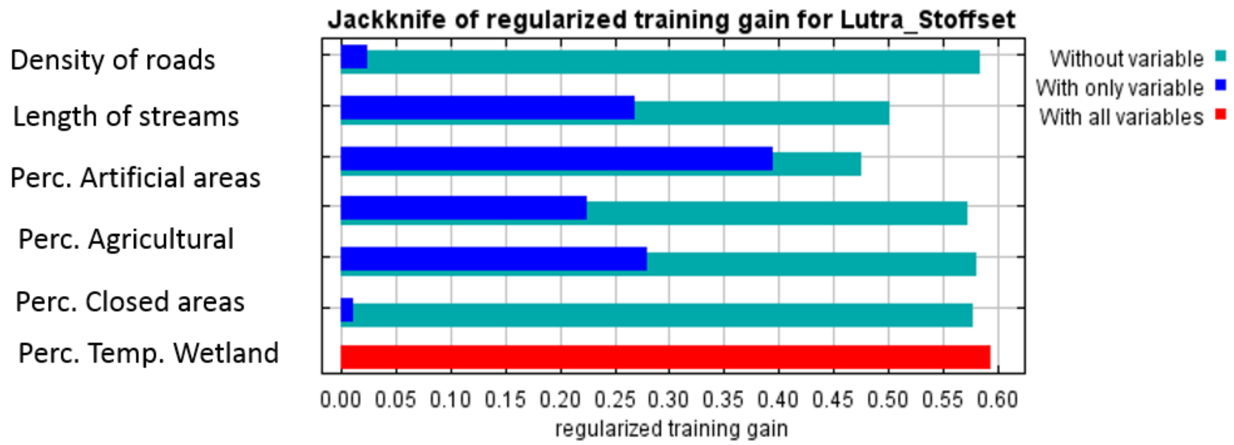
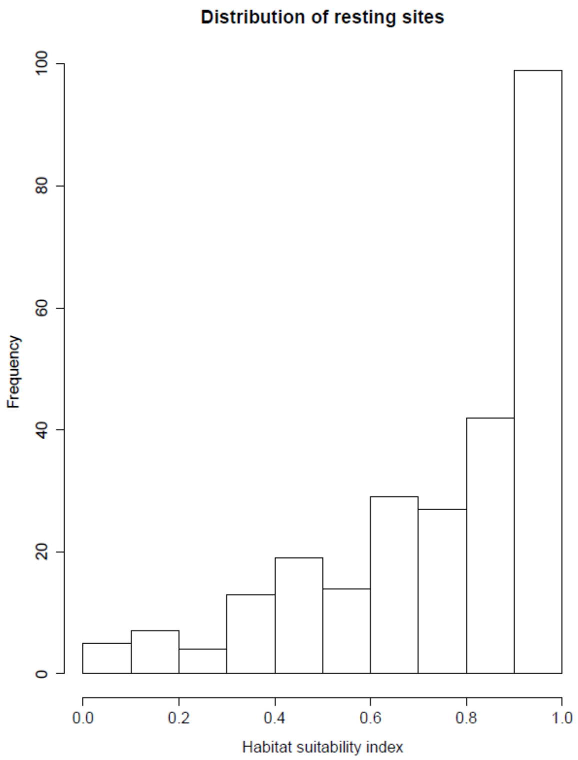


Fig. S1. Result of jackknife test for evaluating the relative contribution of the predictor variables to the habitat model of otters in Austria and Switzerland.

a)



b)

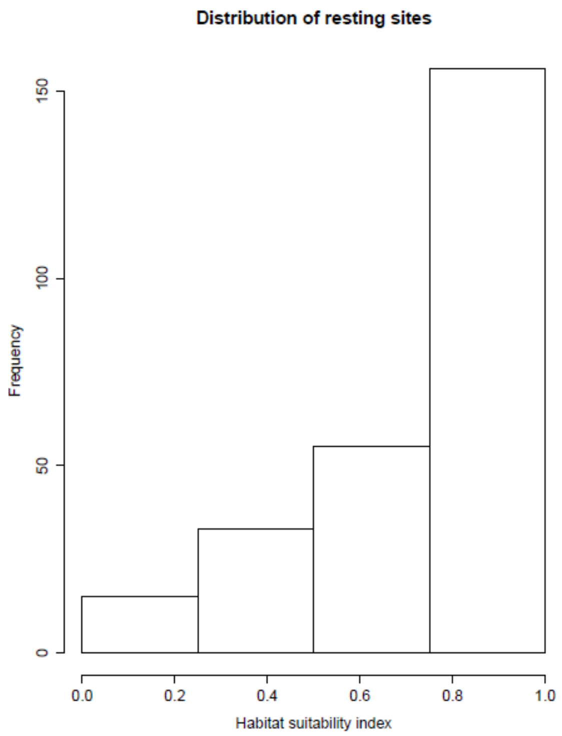
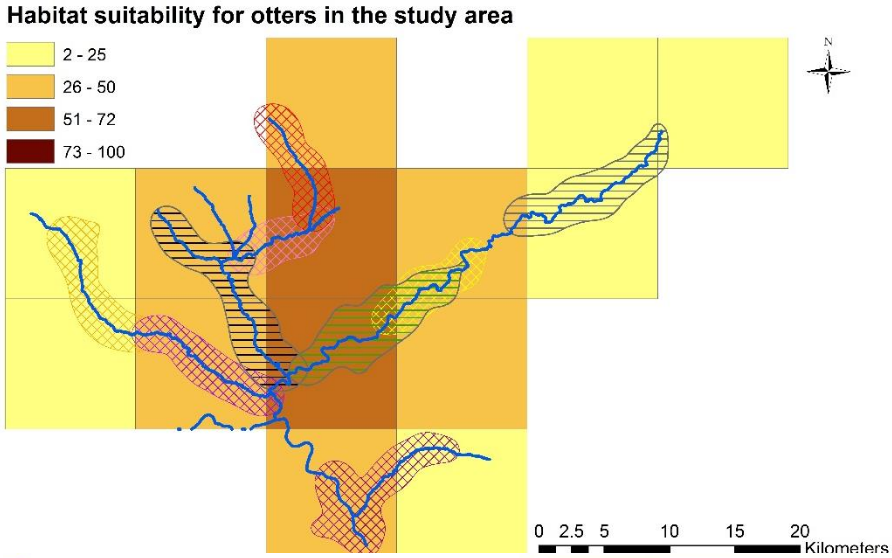


Figure S2a). Distribution of resting sites of radiotracked animals among the calculated HS index at equal sized bins (width of 0.1) in the study area. Figure S2b). Number of the resting sites within equal sized bins with width of 0.25 along the HS Index.



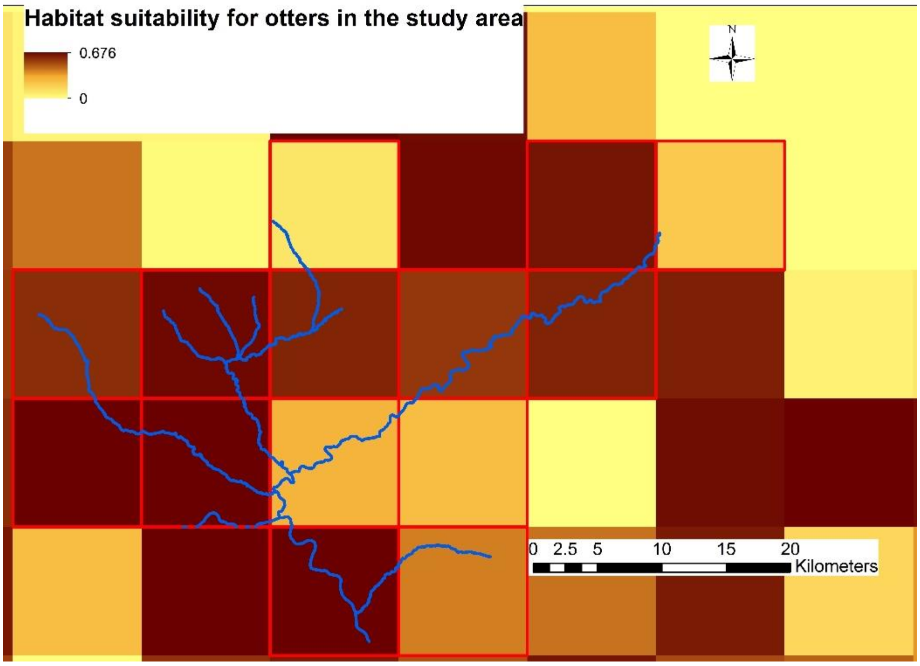


Fig. S3. Habitat suitability at two scales in the study area: fine (above, HIS 0-100) and coarse (below, HIS 0-1), both with a grid of 10 km^2 for comparability. The darker the cell, the more optimal habitat is available. At the fine scale, only the percentage of the best habitat was used. Overlaying there are the home ranges of nine individuals to visualize spatial requirements.

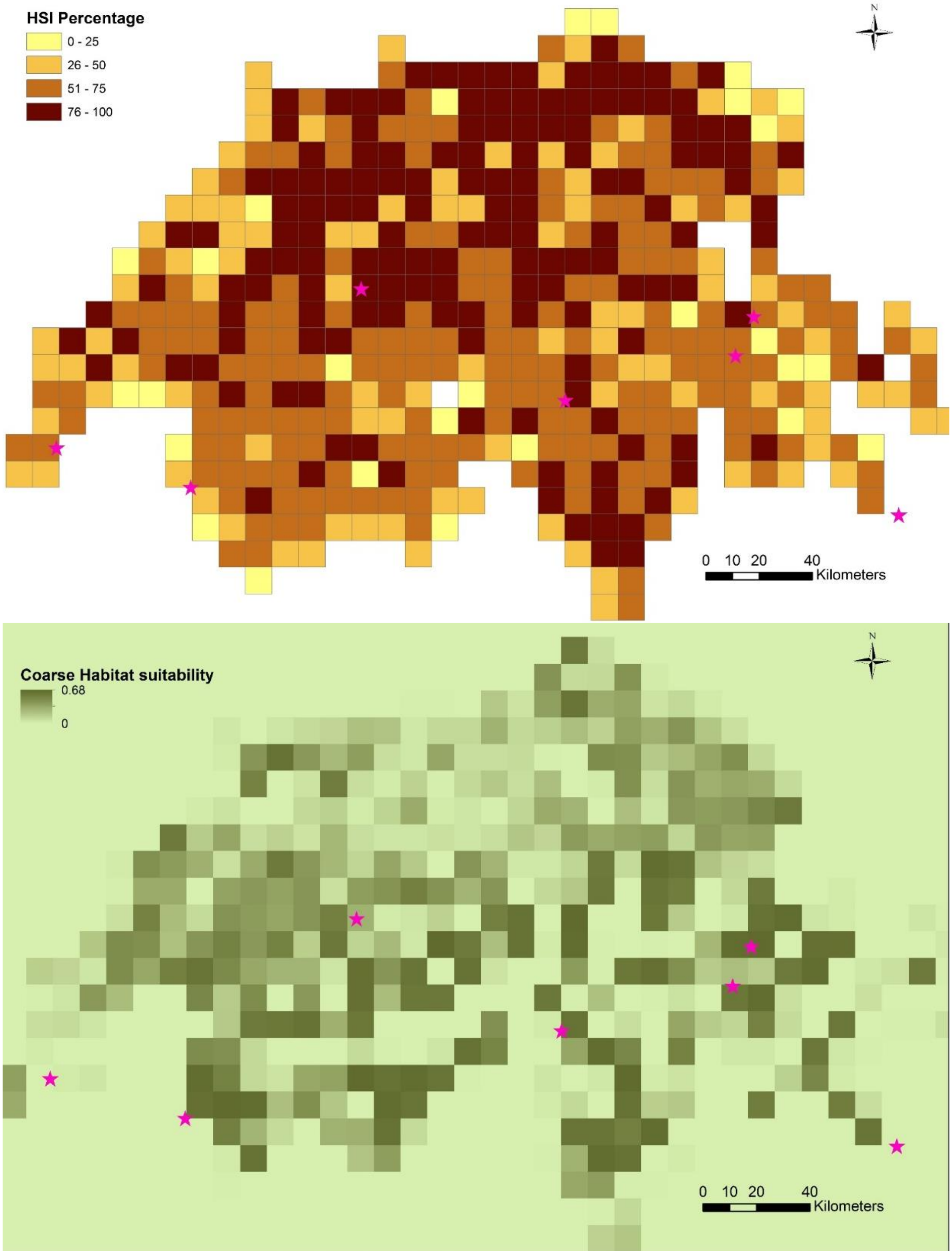


Fig. S4. Habitat suitability at two scales: fine (above, HIS 0-100) and coarse (below, HIS 0-1). Pink stars indicate the location of observations of wild otters in Switzerland (www.prolutra.ch).

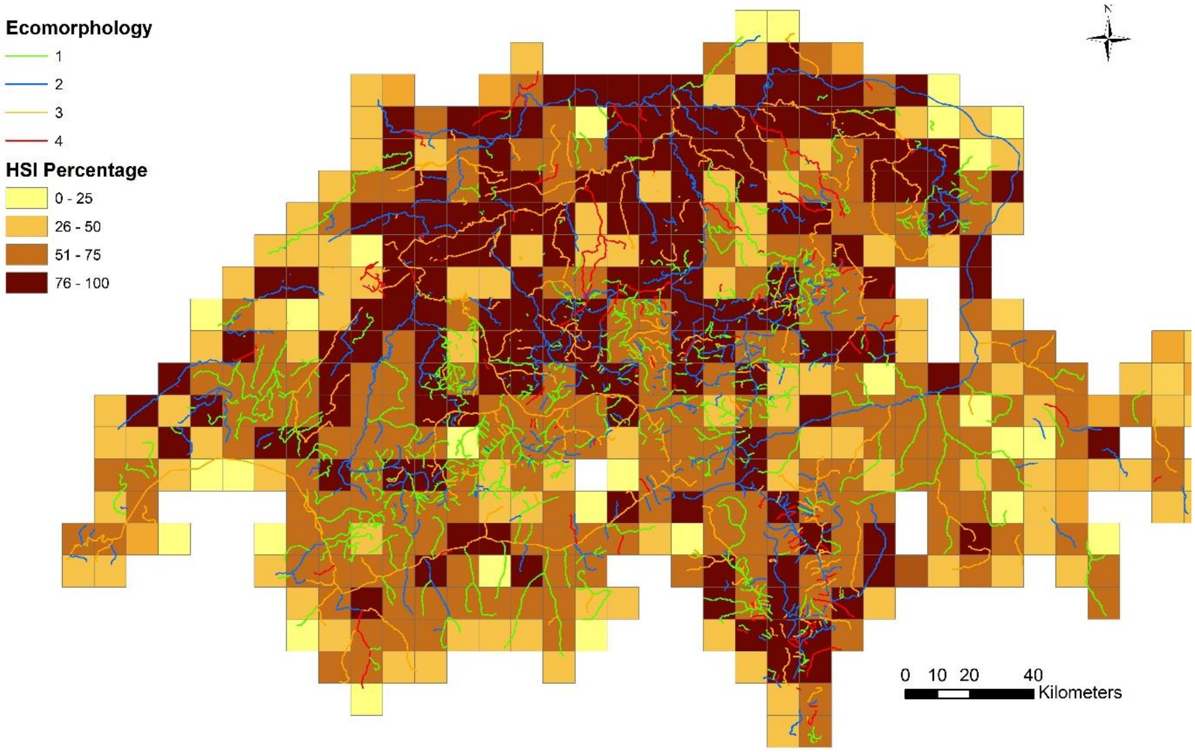


Fig. S5. Fine scale habitat suitability recalculated for 10 km^2. The amount of "suitable habitat" over all habitat has been calculated for each cell. The darker the cells, the higher the estimated habitat suitability. Overlaying are the watercourses (> 4m) of which the ecomorphology had been assessed: green = natural state, blue = semi-natural, orange = non-natural and red = artificial state.

Table A1. Best models for fine scale resting site selection according to the AICc. AICc is the value of the corrected Akaike's Information Criterion, and K is the number of estimated parameters for each model. The ranking of the models is based on differences in the corrected Akaike's Information Criterion (Delta AICc).

Models	AICc (K)	Delta AICc (wi)
NATURALNESS + PAVED ROADS	1628 (6)	0.00 (0.67)
NATURALNESS + ROADS COMBINED	1631 (6)	2.36 (0.21)
VTYPE + PAVED ROADS	1633 (5)	4.96 (0.05)

Models	AICc (K)	Delta AICc (wi)
NATURALNESS + PAVED ROADS	1628 (6)	0.00 (0.67)
NATURALNESS + ROADS COMBINED	1631 (6)	2.36 (0.21)
VTYPE + PAVED ROADS	1633 (5)	4.96 (0.05)

Chapter 5

Conclusions and perspectives

Tony Hisgett

General Discussion and Perspectives

In a world transformed by humans it is important to understand the response of wildlife to those environmental changes and to human presence (Pettifor, Norris & Rowcliffe 2004). This is especially true for endangered species (Blanc *et al.* 2014; Hanson *et al.* 2015; Karmanlidis *et al.* 2015). The identification of suitable habitats contributes furthermore to the protection and recovery of a population or species (Güthlin *et al.* 2011; Carranza *et al.* 2012; Milanesi *et al.* 2015). In my thesis, I investigated the habitat selection of the Eurasian otter after the re-expansion of the species in formerly abandoned habitat. Additionally, I developed habitat suitability models to predict the recovery into the core of the Alpine Arc where the species is at the periphery of the current distribution.

Otters in freshwater ecosystems in Europe are difficult to study due to their nocturnal and secretive life. Thus habitat selection studies of otters often rely on indirect signs with which distinctive behaviour cannot be distinguished (e.g. Almeida et al., 2013; Juhász et al., 2013; Lundy and Montgomery, 2010; Romanowski et al., 2013). However, habitat selection varies between the different behaviours, e.g. roosting behaviour or foraging (Signorell *et al.* 2010; Maltagliati, Agnelli & Cannicci 2013; Oksanen *et al.* 2015). The detailed knowledge on the habitat selection among behaviors can be crucial to understand the spatial distribution and to target efficient conservation actions for species of concern. For elusive and highly mobile species, the application of biotelemetry yields profound insights to spatial requirements and habitat use (Zeale, Davidson-Watts & Jones 2012; Armstrong *et al.* 2013). By radiotracking wild otters in Styria, I collected an extraordinary and extensive data set, where the habitat requirements for distinctive behaviours could be investigated in detail. For my thesis, I focussed on the behaviours of foraging (Chapter 2) and resting (Chapter 3). By differentiating between those main daily activities, I was able to show the contrary effects of a landscape modified by humans to the habitat selection of otters.

Although the importance of the riverine landscape is known (Semlitsch & Bodie 2003; Bennett, Nimmo & Radford 2014), hydropower stations, revetments and a transition of riparian vegetation to settlements, roads or agricultural fields have changed this ecosystem drastically (Comiti 2012). In this altered landscape, otters have re-expanded again (Kranz and Polednik, 2015; Kranz and Toman, 2000; Kranz et al., 2013), thus questioning the notion of otters being linked to pristine and healthy environments (Ruiz-Olmo *et al.* 1998; Bifolchi & Lode 2005). My findings suggest that otters are very flexible in their foraging habitat selection (Chapter 2). By incorporating movement into habitat selection analyses, I show that heavily modified habitat such as reservoirs and residual waters are indeed preferred hunting grounds for otters. However, this preference is most likely caused by fish stocking, which is an old

tradition throughout the Alpine Arc. The numerous barriers such as weirs may cause stocked fish to assemble and become easy prey for fish eating species. Thus, otters may be benefit indeed from strong modifications to the watercourses as long as there is enough prey available. Beyond being a prerequisite for the presence of a carnivore, prey can also structure their home range (Mattisson *et al.* 2013; Newsome *et al.* 2013). Fish abundance has been shown to affect otter density (Ruiz-Olmo *et al.* 2011). Thus, the traditional fish stocking in the Alps may influence home range size of otters and contribute to the population dynamics, but this topic has only received recently attention (Sittenthaler *et al.* 2015). Alternatively, the effect of fish stocking may be diminished by the high plasticity in food types otters can express (Krawczyk *et al.* 2016). Preliminary results of the diet composition of otters in the study area showed a seasonal variation in prey, which included also anurans, birds and crustaceans (see Supplementary Material).
Wildlife preying on game species often leads to human-wildlife conflicts. The otter as an agile and efficient fish hunter can cause conflicts (Kloskowski 2005; Vaclavikova, Vaclavik & Kostkan 2011). Where fish stocking is applied to enhance fishing success, otter presence can quickly lead to negative attitudes toward the species. While some fishponds can be made otter proof, game fish in running waters cannot be protected. Fishing societies and private persons, which rent stretches of streams and rivers to fish, may stop the practice of fish stocking in the presence of otters. This in turn may lead to a reduced availability of prey for otters, e.g. in habitats such as reservoirs, thus changing their habitat selection.

The flexibility in modification of the habitat shifted with the behaviour. Almost exclusively all resting sites of otters were found in the riparian vegetation (Chapter 3). Here, otters use different structures (below and above ground) as resting sites. Thermal coverage has been stressed as one of the main driver for resting site selection in other mustelids (Weber 1989; Baghli & Verhagen 2005). My findings however indicate that protection from disturbance or predation contributes most to the resting site selection. By estimating human disturbance at a very fine scale around each resting site, I show that otters perceive humans as a disturbance or threat and that they choose their resting site accordingly. Riparian vegetation plays a crucial role as it functions as a buffer when human disturbance is high. The impact of human disturbance however goes unnoticed at a larger scale. This may be due to some extent to the fact that although roads can function as a proxy for human disturbance, they give no indication on the intensity of human presence and its prediction (e.g. permanent workers vs people walking their free roaming dog). However, my findings on the resting site selection at a very fine scale indicate that it is exactly this predictability, which is of high importance to resting otters. My results thus emphasize the dependency of resting otters on vegetation cover as a buffer to human disturbance, a relationship also shown in other carnivore species

(Sunde, Stener & Kvam 1998; Ordiz *et al.* 2011; Fernandez-Lopez *et al.* 2014; Sálek *et al.* 2014).

Habitat suitability maps can predict future occurrence of a species and identify barriers or problems (Araújo & Williams 2000; Rushton, Merod & Kerby 2004). The otter, being protected under the EC Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC 1992), has received much attention, which resulted in an abundance of habitat suitability models at local, national and at the European scale (Ottino, Prigioni & Taglianti 1995; Kemenes & Demeter 1995; Klenke 1998; Robitaille & Laurence 2002; Janssens *et al.* 2006; Prigioni, Balestrieri & Remonti 2007; Remonti *et al.* 2008; Loy *et al.* 2009; Marcelli & Fusillo 2009; Ottaviani *et al.* 2009; Cianfrani *et al.* 2010, 2013; Clavero *et al.* 2010; Carranza *et al.* 2012; Marcelli *et al.* 2012; Van Looy *et al.* 2013; Carone *et al.* 2014). As a result of the difficulty to study otters in the wild, the resolution of the models remain often coarse, e.g. national or at the grid size of 10 km^2, which used for the standardized otter survey recommended (Foster-Turley, Macdonald & Mason 1990) and applied in most European countries.
Scale is an important factor in conservation (Cabeza *et al.* 2010). It has been shown that environmental variables may differ in impact and direction depending on the spatial scale (Collingham *et al.* 2000). Grid resolution has an effect on the estimated distribution and abundance of otters and influences even conservation status (Sales-Luis, Bissonette & Santos-Reis 2012). By analyzing habitat selection at different scales and developing two habitat suitability models with different spatial resolution, I acknowledged the importance of the multi-scale approach (du Toit 2010). Both HSMs show that suitable habitat in Switzerland is available for otters (Chapter 4). To build the models, I used data sets from snowtracking surveys and from the radiotracking study. Snowtracking surveys can yield population estimations of otters (Sulkava & Liukko 2007). I was fortunate to be given data on snowtracking surveys done between 2010 and 2013 (Kranz *et al.* 2013). The number of individuals was provided with a resolution of 10 km^2, resulting in the equivalent coarse resolution for environmental variables. Despite of the large data sets collected on many environmental variables and demography by the national offices (e.g. Federal Office for Topography Switzerland or Bundesamt für Eich- und Vermessungswesen, Austria), data on the watercourses and its surrounding riparian landscape is scarce. This scarcity of information on riverine habitat resulted in a HSM with information mainly on the area outside the riparian landscape.
Aiming at a fine scale HSM and its transferability to Switzerland, I collected ecomorphological data on the Austrian streams and rivers in the study area using the methodology of the Federal Office for Environment Switzerland. By building a HSM using the habitat requirements for resting sites, which is the more demanding behavior regarding habitat

quality, I could incorporate the information on riparian landscape. Here, the validation of the HSM was restricted to the study area due to the delimitation of the ecomorphological assessment. Additionally, an extrapolation to other regions without the same assessment is difficult. However, by using and combining the information on the resting site selection at a fine scale (Chapter 3), the potential home range size (Chapter 2) and the distribution of good habitat for resting sites (Chapter 4), local assessments of any given region can be made and effective conservation actions planned.

An important aspect of otter occurrence is prey abundance (Ruiz-Olmo, López-Mart & Palazón 2001). Information on fish biomass covering the study areas was unavailable and thus an incorporation in the HSM was not feasible. In the last few decades, a decline of some Swiss fish populations was observed (Borsuk *et al.* 2006), which could impair recovery of otter populations in Switzerland. Also, it can be expected that fish biomass is influenced by the fish management, e.g. intensity of the fish stocking. Although the tradition of fish stocking is executed in Austria and Switzerland, the practice between the countries most likely differs.

Besides habitat features and prey abundance, pesticides in the water influence otter presence and perseverance. PCB (polychlorinated byphenyl) and DDE (dichlorodiphenyl dichloroethylene), mercury but also new toxic contaminants (e.g perfluorooctane sulfonic acid PFOS and polybrominated diphenyl ethers PBDEs) may threaten otter species (Lodenius *et al.* 2014; Pountney *et al.* 2014; Nelson *et al.* 2015). Data on those aspects proved difficult to obtain in both Austria and Switzerland. However, an incorporation into the existing models would add valuable information on the prediction of persistence of otter occurrence.

Connectivity of suitable habitat is crucial for dispersal (Squires *et al.* 2013; Peters *et al.* 2015). Natal dispersal in otters covers surprisingly short distances (Quaglietta *et al.* 2013) and dispersing individuals may follow mainly watercourses. Thus, horizontal barriers such as weirs or causes for increased mortality like high densities of roads may impact their dispersal ability. A study on the potential of otters to recolonize the Alps indicated a high external and internal permeability of Switzerland (Cianfrani *et al.* 2013). Therefore, I omitted the question of connectivity in the present study. However, habitat avoidances and highly localized barriers such as specific weirs with no possibility for otters to overcome may influence recovery in some areas. Assessment of structures and the local influence of roads, a main cause of mortality shown elsewhere (Philcox, Grogan & Macdonald 1999; Guter *et al.* 2006; Jancke & Giere 2010), would contribute to an effective conservation planning for otters at a local scale in the Alpine Arc.

Altogether, this thesis provides important information for management plans and conservation actions at different scales to preserve and facilitate the recovery of this charismatic semi-aquatic carnivore. Otter sightings started right on cue with the beginning of my thesis in Switzerland (see www.prolutra.ch) and are slowly increase since then. My models contribute to the identification of areas with future otter occurrence, but also point out areas with low habitat suitability at different resolutions. Thus, management actions can be targeted at large scale but also at a very fine scale. Although the work here focused on the alpine landscape, I am certain that those findings are also valid in other regions.

References

92/43/EEC. (1992) Conservation of Natural Habitats and of Wild Fauna and Flora.

Almeida, D., Rodolfo, N., Sayer, C.D. & Copp, G.H. (2013) Seasonal use of ponds as foraging habitat by Eurasian otter with description of an alternative handling technique for common toad predation. *Folia Zoologica*, **62**, 214–221.

Araújo, M.B. & Williams, P.H. (2000) Selecting areas for species persistence using occurrence data. *Biological Conservation*, **96**, 331–345.

Armstrong, D.P., Mcarthur, N., Govella, S., Morgan, K., Johnston, R., Gorman, N., Pike, R. & Richard, Y. (2013) Using radio-tracking data to predict post-release establishment in reintroductions to habitat fragments. *Biological Conservation*, **168**, 152–160.

Baghli, A. & Verhagen, R. (2005) Activity patterns and use of resting sites by polecats in an endangered population. *Mammalia*, **69**, 211–222.

Bennett, A.F., Nimmo, D.G. & Radford, J.Q. (2014) Riparian vegetation has disproportionate benefits for landscape-scale conservation of woodland birds in highly modified environments. J*ournal of Applied Ecology*, 514–523.

Bifolchi, A. & Lode, T. (2005) Efficiency of conservation shortcuts: An investigation with otters as umbrella species. *Biological Conservation*, **126**, 523–527.

Blanc, A., Jago, M., Voigt, C.C., Thalwitzer, S. & Wachter, B. (2014) The Conflict between Cheetahs and Humans on Namibian Farmland Elucidated by Stable Isotope Diet Analysis. *PlosOne*, **9**.

Borsuk, M.E., Reichert, P., Peter, A., Schager, E. & Burkhardt-Holm, P. (2006) Assessing the decline of brown trout (Salmo trutta) in Swiss rivers using a Bayesian probability network. *Ecological Modelling*, **192**, 224–244.

Cabeza, M., Arponen, A., Jäättelä, L., Kujala, H., van Teeffelen, A. & Hanski, I. (2010) Conservation planning with insects at three different spatial scales. *Ecography*, **33**, 54–

63.

Carone, M.T., Guisan, A., Cianfrani, C., Simoniello, T., Loy, A. & Carranza, M.L. (2014) A multi-temporal approach to model endangered species distribution in Europe. The case of the Eurasian otter in Italy. *Ecological Modelling*, **274**, 21–28.

Carranza, M.L., D'Alessandro, E., Saura, S. & Loy, A. (2012) Connectivity providers for semi-aquatic vertebrates: The case of the endangered otter in Italy. *Landscape Ecology*, **27**, 281–290.

Cianfrani, C., Lay, L., Hirzel, A.H. & Loy, A. (2010) Do habitat suitability models reliably predict the recovery areas of threatened species ? *Journal of Applied Ecology*, 421–430.

Cianfrani, C., Maiorano, L., Loy, A., Kranz, A., Lehmann, A., Maggini, R. & Guisan, A. (2013) There and back again? Combining habitat suitability modelling and connectivity analyses to assess a potential return of the otter to Switzerland. *Animal Conservation*, **16**, 584–594.

Clavero, M., Hermoso, V., Brotons, L. & Delibes, M. (2010) Natural, human and spatial constraints to expanding populations of otters in the Iberian Peninsula. *Journal of Biogeography*, **37**, 2345–2357.

Collingham, Y.C., Wadsworth, R.A., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of non-indigenous riparian weeds: Issues of spatial scale and extent. *Journal of Applied Ecology*, **37**, 13–27.

Comiti, F. (2012) How natural are Alpine mountain rivers? Evidence from the Italian Alps. *Earth Surface Processes and Landforms*, **37**, 693–707.

Fernandez-Lopez, J., Fandos, G., Cano, L.S., Garcia, F.J. & Telleria, J.L. (2014) Effect of wildlife refuges on small carnivores in a hunting area in Mediterranean habitat. *Hysterix*, **25**, 45–46.

Foster-Turley, P., Macdonald, S.M. & Mason, C.F. (1990) *Otters: An Action Plan for Their Conservation*. IUCN Otter Specialist Group.

Guter, A., Dolev, A., Saltz, D. & Kronfeld-Schor, N. (2006) Temporal and spatial influences on road mortality in otters: Conservation implications. *Israel Journal of Zoology*, **51**, 199–207.

Güthlin, D., Knauer, F., Kneib, T., Küchenhoff, H., Kaczensky, P., Rauer, G., Jonozovič, M., Mustoni, A. & Jerina, K. (2011) Estimating habitat suitability and potential population size for brown bears in the Eastern Alps. *Biological Conservation*, **144**, 1733–1741.

Hanson, N., Thompson, D., Duck, C., Baxter, J. & Lonergan, M. (2015) Harbour seal (Phoca vitulina) abundance within the Firth of Tay and Eden Estuary, Scotland : recent trends and extrapolation to extinction. Aquatic Conservation: Marine and Freshwater Ecosystems, doi: 10.1002/aqc.2609.

Jancke, S. & Giere, P. (2010) Patterns of otter Lutra lutra road mortality in a landscape abundant in lakes. *European Journal of Wildlife Research,* **57**, 373-381.

Janssens, X., Defourny, P., De Kermabon, J. & Baret, P. (2006) The recovery of the otter in the Cevennes (France): a GIS-based model. *Hystrix*, **17**, 5–14.

Juhász, K., Lukács, B.A., Perpék, M., Nagy, S.A. & Végvári, Z. (2013) Effects of extensive fishpond management and human disturbance factors on Eurasian otter (Lutra lutra L. 1758) populations in Eastern Europe. *North-Western Journal of Zoology*, **9**, 227–238.

Karmanlidis, A.A., Dendrinos, P., de Larrinoa, P.F., Gücü, A.C., Johnson, W.M., Kiraç Sad, C.O. & Pires, R. (2015) The Mediterranean monk seal Monachus monachus : status, biology, threats, and conservation priorities. *Mammal Review,* **46**, 92-105.

Kemenes, I. & Demeter, A. (1995) A predictive model of the effect of environmental factors on the occurrence of otters (Lutra lutra L.) in Hungary. *Hystrix*, **7**, 209–218.

Klenke, R. (1998) Habitat suitability and apparent density of the Eurasian otter (Lutra lutra) in Saxony (Germany). *IUCN Otter Specialist Group Bulletin*, **19**, 167–171.

Kloskowski, J. (2005) Otter Lutra lutra damage at farmed fisheries in southeastern Poland, I: an interview survey. *Wildlife Biology*, **11**, 201–206.

Kranz, A. & Polednik, L. (2015) *Fischotter in Kaernten: Verbreitung & Bestand 2014. Endbericht im Auftrag des Amtes der Kaerntner Landesregierung*. Graz.

Kranz, A., Polednik, L., Pavanello, M. & Kranz, I. (2013) *Fischotterbestand in der Steiermark - Spurschneekartierungen 2010 - 2013. Endbericht.* Graz.

Kranz, A. & Toman, A. (2000) Otters recovering in man-made habitats in central Europe. *Mustelids in a modern world*, Huw I. Gri (ed H.I. Griffiths), pp. 163–184. Bachhuys Publishers, Leiden, Netherlands.

Krawczyk, A.J., Bogdziewicz, M., Majkowska, K. & Glazaczow, A. (2016) Diet composition of the Eurasian otter Lutra lutra in different freshwater habitats of temperate Europe: a review and meta-analysis. *Mammal Review,* **46**, 106-113.

Lodenius, M., Skarén, U., Hellstedt, P. & Tulisalo, E. (2014) Mercury in various tissues of three mustelid species and other trace metals in liver of European otter from Eastern Finland. *Environmental monitoring and assessment*, **186**, 325–33.

Van Looy, K., Cavillon, C., Tormos, T., Piffady, J., Landry, P. & Souchon, Y. (2013) A scale-sensitive connectivity analysis to identify ecological networks and conservation value in river networks. *Landscape Ecology*, **28**, 1239–1249.

Loy, A., Carranza, M., Cianfrani, C., D'Alessandro, E., Bonesi, L., Di Marzio, P., Minotti, M. & Reggiani, G. (2009) Otter Lutra lutra population expansion: Assessing habitat suitability and connectivity in southern Italy. *Folia Zoologica*, **58**, 309–326.

Lundy, M.G. & Montgomery, W.I. (2010) A multi-scale analysis of the habitat associations of European otter and American mink and the implications for farm scale conservation schemes. *Biodiversity and Conservation*, **19**, 3849–3859.

Maltagliati, G., Agnelli, P. & Cannicci, S. (2013) Where and at What Time ? Multiple Roost use and Emergence Time in Greater Horseshoe Bats (Rhinolophus ferrumequinum).

Acta chiropterologica, **15**, 113–120.

Marcelli, M. & Fusillo, R. (2009) Assessing range re-expansion and recolonization of human-impacted landscapes by threatened species: a case study of the otter (Lutra lutra) in Italy. *Biodiversity and Conservation*, **18**, 2941–2959.

Marcelli, M., Poledník, L., Poledníková, K. & Fusillo, R. (2012) Land use drivers of species re-expansion: inferring colonization dynamics in Eurasian otters. *Diversity and Distributions*, **18**, 1001–1012.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R. & Pedersen, H.C. (2013) Home range size variation in a recovering wolf population : evaluating the effect of environmental, demographic, and social factors. *Oecologia*, **173**, 813–825.

Milanesi, P., Caniglia, R., Fabbri, E., Galaverni, M., Meriggi, A. & Randi, E. (2015) Non-invasive genetic sampling to predict wolf distribution and habitat suitability in the Northern Italian Apennines: implications for livestock depredation risk. *European Journal of Wildlife Research*, **61**, 681–689.

Nelson, C., Drouillard, K., Cheng, K., Elliott, J. & Ismail, N. (2015) Accumulation of PBDEs in an urban river otter population and an unusual finding of BDE-209. *Chemosphere,* **118**, 322–328.

Newsome, T.M., Ballard, G., Dickman, C.R., Fleming, P.J.S. & Ven, R. Van De. (2013) Home range , activity and sociality of a top predator, the dingo : a test of the Resource Dispersion Hypothesis. *Ecography*, **36**, 914–925.

Oksanen, S.M., Niemi, M., Ahola, M.P. & Kunnasranta, M. (2015) Identifying foraging habitats of Baltic ringed seals using movement data. *Movement Ecology*, 1–11.

Ordiz, A., Stoen, O.-G., Delibs, M. & Swenson, J.E. (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, **166**, 59–67.

Ottaviani, D., Panzacchi, M., Jona Lasinio, G., Genovesi, P., Boitani, L., Lasinio, G.J. & Jonalasinio, G. (2009) Modelling semi-aquatic vertebrates' distribution at the drainage basin scale: The case of the otter Lutra lutra in Italy. *Ecological Modelling*, **220**, 111–121.

Ottino, P., Prigioni, C. & Taglianti, V. (1995) Habitat suitability for the otter (Lutra lutra) of some rivers of Abruzzo region (central Italy). *Hysterix*, **7**, 265–268.

Peters, W., Hebblewhite, M., Cavedon, M., Pedrotti, L., Mustoni, A., Zibordi, F., Groff, C., Zanin, M. & Cagnacci, F. (2015) Resource selection and connectivity reveal conservation challenges for reintroduced brown bears in the Italian Alps. *Biological Conservation*, **186**, 123–133.

Pettifor, R.A., Norris, K.J. & Rowcliffe, J.M. (2004) Incorporating behaviour in predictive models for conservation. *Behaviour and Conservation* (eds L.M. Gosling), & W.J. Sutherland), pp. 198–220. Cambrige University Press, Cambridge.

Philcox, C.K.K., Grogan, a. L.L. & Macdonald, D.W.W. (1999) Patterns of otter Lutra lutra road mortality in Britain. *Journal of Applied Ecology*, **36**, 748–761.

Pountney, A., Filby, A.L., Thomas, G.O., Simpson, V.R., Chadwick, E. A, Stevens, J.R. & Tyler, C.R. (2014) High liver content of polybrominated diphenyl ether (PBDE) in otters (Lutra lutra) from England and Wales. *Chemosphere*, **118C**, 81–86.

Prigioni, C., Balestrieri, A. & Remonti, L. (2007) Decline and recovery in otter Lutra lutra populations in Italy. *Mammal Review*, **37**, 71–79.

Quaglietta, L., Fonseca, V.C., Hájková, P., Mira, A. & Boitani, L. (2013) Fine-scale population genetic structure and short-range sex-biased dispersal in a solitary carnivore, *Lutra lutra*. *Journal of Mammalogy*, **94**, 561–571.

Remonti, L., Prigioni, C., Balestrieri, A., Sgrosso, S. & Priore, G. (2008) Distribution of a recolonising species may not reflect habitat suitability alone: The case of the Eurasian otter (Lutra lutra) in southern Italy. *Wildlife Research*, **35**, 798–805.

Robitaille, J.F. & Laurence, S. (2002) Otter, Lutra lutra, occurrence in Europe and in France in relation to landscape characteristics. *Animal Conservation*, **5**, 337–344.

Romanowski, J., Brzeziński, M. & Zmihorski, M. (2013) Habitat correlates of the Eurasian otter Lutra lutra recolonizing Central Poland. *Acta theriologica*, **58**, 149–155.

Ruiz-Olmo, J., Batet, A., Mañas, F. & Martínez-Vidal, R. (2011) Factors affecting otter (Lutra lutra) abundance and breeding success in freshwater habitats of the northeastern Iberian Peninsula. *European Journal of Wildlife Research*, **57**, 827–842.

Ruiz-Olmo, J., Calvo, A., Palazón, S. & Arqued, V. (1998) Is the Otter a bioindicator. *Galemys*, 227–237.

Ruiz-Olmo, J., López-Mart, J.M. & Palazón, S. (2001) The influence of fish abundance on the otter (Lutra lutra) populations in Iberian Mediterranean habitats. *Journal of Zoology, London*, **254**, 325–336.

Rushton, S.P., Merod, S.J.O.R. & Kerby, G. (2004) New paradigms for modelling species distributions ? *Journal of Applied Ecology*, **41**, 193–200.

Sálek, M., Cervinka, J., Pavluvˇ, P., Poláková, S. & Tkadlec, E. (2014) Forest-edge utilization by carnivores in relation to local and landscape habitat characteristics in central European farmland. *Mammalian Biologie - Zeitschrift fuer Saeugetierkunde*, **79**, 176–182.

Sales-Luis, T., Bissonette, J.A. & Santos-Reis, M. (2012) Conservation of Mediterranean otters : the influence of map scale resolution. *Biodiversity and Conservation*, **21**, 2061–2073.

Semlitsch, R.D. & Bodie, J.R. (2003) Biological Criteria for Buffer Zones around Wetlands and Riparian Habitats for Amphibians and Reptiles. *Conservation Biology*, **17**, 1219–1228.

Signorell, N., Wirthner, S., Patthey, P., Schranz, R. & Arlettaz, R. (2010) Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse Tetrao tetrix hens : habitat management implications Original article Concealment from predators drives foraging habitat selection in brood-rearing Alpine bl. *Wildlife Biology*, **16**, 249–257.

Sittenthaler, M., Bayerl, H., Unfer, G., Kuehn, R. & Parz-Gollner, R. (2015) Impact of fish stocking on Eurasian otter (Lutra lutra) densities: A case study on two salmonid streams Author: *Mammalian Biology*, **80**, 106–113.

Squires, J.R., DeCesare, N.J., Olson, L.E., Kolbe, J. a., Hebblewhite, M. & Parks, S. a. (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. *Biological Conservation*, **157**, 187–195.

Sulkava, R.T. & Liukko, U.M. (2007) Use of snow-tracking methods to estimate the abundance of otter (Lutra lutra) in Finland with evaluation of one-visit census for monitoring purposes. *Annales Zoologici Fennici*, **44**, 179–188.

Sunde, P., Stener, S.O. & Kvam, T. (1998) Tolerance to humans of resting lynxes Lynx lynx in a hunted population. *Wildlife Biology*, **4**, 177 – 183.

du Toit, J.T. (2010) Considerations of scale in biodiversity conservation. *Animal Conservation*, **13**, 229–236.

Vaclavikova, M., Vaclavik, T. & Kostkan, V. (2011) Otters vs. fishermen: Stakeholders' perceptions of otter predation and damage compensation in the Czech Republic. *Journal for Nature Conservation*, **19**, 95–102.

Weber, D. (1989) The ecological significance of resting sites and the seasonal haibtat change in polecats (Mustela putorius). *Journal of Zoology London*, **217**, 629–638.

Zeale, M.R.K., Davidson-Watts, I. & Jones, G. (2012) Home range use and habitat selection by barbastelle bats (Barbastella barbastellus): implications for conservation. *Journal of Mammalogy*, **93**, 1110–1118.

Addresses of Co-Authors

Fabio Bontadina

SWILD – Urban Ecology & Wildlife Research
Wuhrstr. 12
8003 Zurich
Switzerland

Swiss Federal Research Institute WSL
Biodiversity and Conservation Biology
8903 Birmensdorf
Switzerland

Addy de Jongh

Dutch Otterstation Foundation
Spanjaardslaan 136
8917 AX Leeuwarden
Netherlands

Andreas Kranz

alka-kranz Ingenieurbüro für Wildökologie und Naturschutz
Am Waldgrund 25
8044 Graz
Austria

Stefanie Muff

Institute of Ecology and Evolutionary Biology,
University of Zurich
Winterthurerstr. 190
8057 Zurich
Switzerland

Epidemiology, Biostatistics and Prevention Institute
University of Zurich
Hirschengraben 84
8001 Zurich
Switzerland

Curriculum Vitae

Personal Data

Surname	Weinberger
Name:	Irene Claudia
Birth	6th February 1976
Nationality	Zug ZG

Education

2010 – 2016	PhD student at the Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland PhD thesis: “The Eurasian Otter (*Lutra lutra*) in the Alpine Arc: Resource selection and habitat suitability models” Supervision: Dr. Fabio Bontadina, Dr. Andreas Kranz and Prof. Dr. Lukas Keller
2002 – 2007	Studies in Biology at the University of Bern, Switzerland Master thesis: “Translocation of bats – a useful conservation tool to augment relict colonies of the two horseshoe bat species in Switzerland?” Supervision: Prof. Dr. Raphaël Arlettaz and Dr. Fabio Bontadina
1998 - 2001	Kantonale Maturitätschule für Erwachsene kme (High school for adults) in Zurich, Switzerland
1993 – 1996	Apprenticeship as office worker, graduated in 1996

Professional activity (excerpt 2010-2016)

2009 –	Self-employed biologist

Acknowledgements

Some many years back, a boss of mine, Lenie, told me to go back to school and study and to do something with my life. I, on the other hand, felt perfectly fine floating around the world, working in wildlife rehab centers and assisting in wildlife research projects. It took me another 1.5 years to start considering her words in earnest. I am glad, I did. This PhD thesis is one of many milestones along my path – and it proved to be one of the most challenging so far. I have met amazing people, had intensive times and learnt a lot of the nature, science and mankind.

This thesis would never been possible without the contribution and support of many people and organisations. I am very grateful to all of them. Thank you!

Pro Lutra initiated, organized and fundraised this project, which we all call proudly "Lutra alpina". Thank you for this wonderful opportunity to do a PhD in such an applied context! I especially thank Sandra Gloor and Hans Schmid for their positive attitudes. They believed in me with such an utter confidence at any time of this thesis, it was actually impossible not to believe them.

I thank Fabio Bontadina, Andreas Kranz and Lukas Keller for their supervision: I thank Andreas for introducing me to the otter world. There is still much to learn, but I hope I have some good solid background. Thank you for sharing your knowledge and data. I thank Fabio for guidance, support and for his keen eye for details. Without you, some things would have been impossible. Thank you! I am grateful to Lukas for having given me a scientific home, a real desk for the duration of this thesis and a helping hand whenever needed.

Many thanks also to the additional members of my PhD comitee: Barbara König and Margarida Santos-Reis. I am glad to have had you in this comitee. I appreciated your inputs, your ideas and support very much. Thank you for your time and thoughts.

Working as a field assistant in this project meant long, cold nights radiotracking otters, helping with habitat assessment during the day, endless data entry – and living in the same apartment as your PhD student boss without escape for months. I do admire all of you. You worked hard, you were ready to jump to chores outside the scope and – and that is the best - you had this infectious laughter you spilled so freely! During this thesis I have met very fine people and I am glad to call some of them today my friends. Thank you all for having been there with me: Ales Toman, André Weller, Anja Hohl, Anja Roy, Annette Stephani, Barbara Schnüriger, Florian Soritz, Gaspar Camlik, Gert Niederkofler, Iris Hanetseder, Jelena Mausbach, Katharina Wagner, Lisa Spühler, Lorena Marconi, Lukas Polednik, Manuel Freiburghaus, Marco Pavanello, Sophie Theunissen, Susana Freire, Susanne Egli (born Pusch), Tabea Lanz, Vasek Beran and Yves Schweizer.

A great thank you to Johanna and Ludwig Kammerhofer who hosted the field station for a few months in that lovely flat in your beautiful house. Thank you for treating us all like family and letting me and my field assistants be part of many great adventures. I won't forget hopping with Ludwig through the dark forest to get close to a great capercaillie!
I thank also the veterinarians Gert Kaltenegger, Ivanna Antos and Christa Weissenbacher, who dedicated time and energy to the wellbeing of the caught otters. Besides running your clinics, you had several weeks during my PhD where you were on stand-by for the surgery and ready at any time of the night. I especially thank Ivanna for taking me out once in a while to get some real Styrian food and do some socializing. I loved it.
I am very grateful to know the finest statisticians. I thank Fränzi Korner-Nievergelt and Tobias for simplifying the statistical world for me and get a glimpse of how cool it actually is. I am very indebted to John Fieberg who has been there at a very critical moment and later created one of the best graphs ever during a conference where there was literally no time. Last but not least at the statistic front: I don't know what I would have done without my co-author Stefanie Muff. Smart, witty and extremely funny, she sailed the statistical sea with me. Now that our Wednesdays are past, let's do some annual retreats.
I felt very much at home in my office group with whom I shared the best office with the nicest view and a tendency towards a jungle. Besides being almost exclusively female, this room harbored a high number of people actively pursuing start-ups. I hope to meet you again as partners! Thanks for the talks, the laughter and your craziness: Alex, Christine, Jasmine, Silvia, Barbara, Kasia and Leyla.
I thank the whole group of Lukas Keller very much. I could walk into your offices at any time of the day with any given type of question – and you seemed literally to drop things to help me. You most likely have no idea how much I appreciated it and how much you helped me. Thank you Andres, Beatrice, Dominique, Eric, Franziska, Glauco, Josh, Judith, Manuela, Mireille, Nina, Philipp, Pirmin, Rasim, Rien, Timothée, Ursina and Vanja.
I specially want to thank Beni Gehr and Mirco Lauper for their time, the discussions and their friendship. While Mirco has fledged, I can't wait for Beni to start a new chapter and invite me to join as a humble field assistant. I want to thank Gabriele Cozzi for a common passion on carnivores (his carnivore species a bit larger than mine, though), the discussions and for setting up the Movement Workshop where I met people who encouraged me on my path. Thanks to Isabel, Susan, Ursina and Barbara for guiding me through the administrative labyrinth and caring for my (financial) wellbeing. Thanks to Michel for spending so much time setting up my PCs and enlarging my horizon substantially on many IT aspects, incl. security.
I also thank all the people who have followed my PhD from a complete different side. I thank my friends, my roomies, my colleagues at work and my family. You all were always interested in my thesis, its progresses, successes and problems. With never ceasing patience you listened to my lengthy explanations of any aspect I just focused on, you

cheered me up and supported me at any time. I am extremely fortunate to have you as friends: Petra, Angie, Barbara, Rahel, Stufi, Fabi, Sime, Oli, Marco, Zsuszi, Anita, Marcella, Trine, Stefe, Monique and Helen. Thanks to my former roomies whom I left during this thesis after years of living together and with whom I am still connected by friendship: Luki, Erich, Claudia J., Claudia M., Remo, Stufi, Fabienne, Bäne, Adi, Barbara, Mera, Vanja, Irina Olga, Mbye, Oli, Joana, Rahel, Kai and Ivi. And last, I thank my family for their support, emotionally and financially, and their constant love during all this time. Thank you very much! I hope you like it.

Supplementary Part Prey selection

Human wildlife conflicts can arise through competition for food resources and can be seen in many carnivore species (Treves & Karanth 2003). In European freshwater systems, fish-eating species such as cormorants, blue herons and otters can be perceived as a threat to anglers and owners of fishponds. In European freshwater systems, the European otter feeds mainly on fish (Krawczyk *et al.* 2016). Studies have shown that otters prefer to feed on cyprinids and slower moving fish (Mason & MacDonald 1986) but also prey on brown trout (*Salmo trutta*) even though these are more demanding to catch (Carss, Kruuk & Conroy 1990). From the turn of the last century, the otter was heavily persecuted, e.g. in Switzerland, and it populations were largely diminished by the mid 20th century. A mix of environmental pollutants, habitat transformation and a lasting effect of the persecution brought the species to a local extinction that spanned most of the Alpine Arc.

In the Alps, the tradition of stocking of fish is old. Enhancement of recreational fisheries was the purpose of the stockings. However, in recent years, stocking has been used increasingly as a conservation tool, both to support native populations by stocking offspring of local wild fish and for the re-establishment of populations where the native populations have been extirpated.

In the last few decades, the otter has expanded its distribution again and occurs today in large parts of Austria (Kranz & Polednik 2015), reheating the human-wildlife conflict again. As shown in a study in Scottish rivers, otters may consume up to 60% of the annual production of juvenile salmonid species (Kruuk *et al.* 1993). As trout is one of the main stocked fish species in the Alps, it is unclear how large the impact of otters is on native and stocked fish. So far, only one study has addressed the influence of otters on stocked fish, by investigating fish biomass (Sittenthaler *et al.* 2015). As a complementary work, I wanted to investigate the correlation between fish stocking events, foraging behavior of otters during that time and prey selection over time. Although I tried for several years to get the data, I could not get hold on neither data on the times of fish stocking not the amount and species of stocked fish. Nevertheless, we collected spraints (faeces) in the territories of the radiotracked otters on a regular basis, thus giving an approximate idea of their seasonal prey.

Methods

Between November 2010 and March 2013, otter faeces (spraints) were collected during bi-monthly surveys on known latrines sites of 9 radiotracked otters in Styria, Austria. All fresh spraints were individually stored in dry plastic bags, labelled with date and in which home range the spraint was situated. The spraints were then stored in the freezer until it was analyzed in the lab. In the laboratory, spraints were dissolved for at least 1h in a detergent solution, washed through a 1mm sieve and the remains were analysed. Fish remains were identified using jay bones, pharyngeal bones, opercula, vertebrae and scales with the aid of available identification keys (Conroy et al, 1993). Additionally, fish remains were compared with a prototype collection of the IPNA in Basel. Crayfish were identified by the presence of characteristic exoskeleton pieces. Amphibians, mammals, birds and reptiles were only identified as such. Whenever possible, prey remains were identified to species level, but identification was always possible to the class level. The minimum number of individuals consumed was calculated by counting and then transposed to the proportion within the spraints. Spraints were grouped as stemming from large rivers (approx. 20m large) and streams (approx. < 20m). They were then analysed separately in seasons (March-May, June-August, September-November, December-February).

Results

Altogether 690 spraints were collected over the time. 532 were found in the streams (< 20m), 152 spraints were collected along the rivers (> 20 m). Within streams and rivers, the number of spraints collected throughout the seasons remained more or less constant (Streams: min= 100, max= 158, rivers: min = 30, max. 52). Otters fed mainly on fish, but also preyed upon arthropods, birds, crustaceans and amphibians. Percentage of salmonids varied among seasons but reached max. 1/3 of the total amount of prey remains per season in any of the watercourses (Table 1). Interestingly, the intake of European bullheads in rivers seems to fluctuate in negative correlation to the amount of salmonids. Remains of sticklebacks were only in territories of streams. In both habitats (rivers and streams), birds were only eaten in spring, while crustaceans and anurans were found throughout the year.

Table 1. Overview of the prey analyses, depending on season and width of watercourse (above) and on season only (below).

Season	Size of watercourse	Salmonidae	Cyprinidae	*Cottus gobio*	Cottus/Perca	Perca	*Gasterosteus aculeatus*	Amphibians	Crustacea	Arthopods	Birds	Other	No of Spraints
Autumn	large > 20m	34.67	0.00	43.00	3.33	3.33	0.00	1.67	9.33	2.67	0.00	2.00	30
	small < 20 m	56.04	0.70	19.49	2.15	0.00	1.84	14.94	1.96	2.25	0.00	0.63	158
Spring	large > 20m	32.26	0.00	35.16	10.00	0.00	0.00	13.55	7.74	1.29	0.00	0.00	31
	small < 20 m	51.34	0.57	18.98	7.15	0.00	1.87	14.72	0.00	3.74	0.00	1.63	123
Summer	large > 20m	20.51	5.38	41.54	19.49	0.00	0.00	0.26	8.97	1.79	2.05	0.00	39
	small < 20 m	60.27	1.68	11.28	7.32	0.00	0.00	10.34	0.54	7.85	0.67	0.07	151
Winter	large > 20m	47.88	1.92	39.62	2.31	0.00	0.00	1.15	6.73	0.38	0.00	0.00	52
	small < 20 m	58.20	0.00	25.70	4.20	0.00	0.90	8.80	0.00	1.50	0.70	0.00	100

Season	Size of watercourse	Salmonidae	Cyprinidae	*Cottus gobio*	Cottus/Perca	Perca	*Gasterosteus aculeatus*	Amphibians	Crustacea	Arthopods	Birds	Other	No of Spraints
Autumn	all combined	52.63	0.59	23.24	2.34	0.53	1.54	12.82	3.14	2.31	0.00	0.85	188
Spring	all combined	47.50	0.45	22.24	7.73	0.00	1.49	14.48	1.56	3.25	0.00	1.30	154
Summer	all combined	52.02	2.45	17.55	9.84	0.00	0.00	8.24	2.29	6.60	0.96	0.05	190
Winter	all combined	54.67	0.66	30.46	3.55	0.00	0.59	6.18	2.30	1.12	0.46	0.00	152
Year	all combined	51.76	1.09	23.06	5.89	0.15	0.89	10.45	2.36	3.44	0.37	0.54	684

References

Carss, D. N., H. Kruuk, and J. W. H. Conroy. 1990. Predation on adult Atlantic salmon, Salmo salar L., by otters, Lutra lutra (L.), within the River Dee system, Aberdeenshire, Scotland. *Journal of Fish Biology* **37**:935–944.

Kranz, A., and L. Polednik. 2015. *Fischotter in Kaernten: Verbreitung & Bestand 2014*. Endbericht im Auftrag des Amtes der Kaerntner Landesregierung. Graz.

Krawczyk, A. J., M. Bogdziewicz, K. Majkowska, and A. Glazaczow. 2016. Diet composition of the Eurasian otter Lutra lutra in different freshwater habitats of temperate Europe: a review and meta-analysis. *Mammal Review,* **46**, 106-113.

Kruuk, H., D. Carss, J. Conroy, and L. Durbin. 1993. Otter (Lutra lutra L.) numbers and fish productivity in rivers in north-east Scotland. *Symposia Zoological Society of London* **65**:171–191.

Mason, C. F., and S. M. MacDonald. 1986. *Otters: Ecology and Conservation*. Cambrige University Press, New York.

Sittenthaler, M., H. Bayerl, G. Unfer, R. Kuehn, and R. Parz-Gollner. 2015. Impact of fish stocking on Eurasian otter (Lutra lutra) densities: A case study on two salmonid streams *Mammalian Biology* **80**:106–113.

Treves, A., and K. U. Karanth. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology*, **17**:1491–1499.